NORTHERN BOBWHITE BROOD ECOLOGY AND POPULATION DYNAMICS IN SOUTHWEST MISSOURI

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by

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and hereby certify that, in their opinion, it is worthy of acceptance.

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DEDICATION

Rachel, Oscar, Joe, Rich, and Jane Sinnott. Ryan King and Buddy "Trouble" Sinnott.

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DISSERTATION ABSTRACT

Northern bobwhite (*Colinus virginianus*) have experienced widespread, long-term population declines. Bobwhite populations in Missouri have declined 2.7% annually between 1966 and 2015, and 3.5% annually between 2005 and 2015, for a cumulative loss of 80% since 1966. Maintaining healthy populations requires a better understanding of how population growth and vital rates across seasons are affected by habitat and land management practices. We examined bobwhite brood ecology and population dynamics in southwest Missouri. My dissertation objectives were to: (1) Examine the influence of cover type, management, and weather on juvenile bobwhite body condition; (2) Estimate bobwhite juvenile survival from hatch as a function of herbaceous cover, habitat management practices, woody vegetation structure, and landscape patterns; (3) Determine population-level bobwhite brood resource selection patterns for managed grasslands and agricultural habitat; and (4) Estimate site-specific bobwhite fecundity, seasonal age- and sex-specific survival, and the relative contributions of these vital rates to trends in abundance.

Among our five study sites, Wade and June Shelton Memorial Conservation Area, Stony Point Prairie Conservation Area, and Wah'Kon-Tah Prairie are native grasslands ranging in size from 320 to 3030 acres. These sites were considered extensively managed, with fire, grazing, mowing and haying implemented to maintain continuous tracts of native grasslands. By contrast, Robert E. Talbot and Shawnee Trail conservation areas (3635–4361 acres) are intensively managed sites. In addition to grassland habitats, both of these areas incorporated small units of agriculture, food plots, and woody vegetation strips for wildlife use.

We used radio telemetry and brood capture data to evaluate the influence of habitat management on juvenile body condition, survival, and brood habitat selection patterns. Brood attending adults were tracked daily from nest hatch to brood capture at approximately 3-weeks old. On capture, juveniles were fitted with transmitters and observed through the life of the bird or the life of the transmitter. Habitat was characterized using maps of herbaceous cover (native- mixed- and cool-season-grasslands, and agricultural cover), management activities (prescribed burning, conservation grazing, mowing/haying), and woody vegetation structure (shrub and tree cover).

To evaluate environmental influencers on bobwhite juvenile body condition, we captured 216 individuals from 33 broods >16-days old across our study sites in 2017 and 2018. We used the residuals from a linear regression of tarsus length and body mass as an index of body condition in a generalized linear mixed model evaluating effects of season, weather, and habitat. We found some support for improved body condition early in the breeding season, under warmer average temperatures, and in native grasslands that were burned and grazed in the previous two years.

We estimated bobwhite juvenile survival based on observations of 705 individuals from 75 broods for a total of 14,904 exposure days. This included 493 individuals observed from hatch to capture and 212 radio-tagged individuals. We estimated 28.6% 114-day period survival for juvenile bobwhite 2016–2018. Survival was highest on native grasslands burned and grazed at least once in the previous two years and survival increased with local shrub cover. Local agricultural cover also improved survival,

however landscape interactions suggest survival is low in small units of cultivated crops surrounded by grasslands or woody vegetation.

We evaluated patterns in brood resource selection and the effects of those choices on brood survival using integrated step selection analysis. We quantified resource selection behavior of 101 bobwhite broods by comparing each of 2,788 chosen daily steps to 10 random available steps not taken. Consistent with our body condition and survival results, native grasslands that were burned and grazed at least once in the previous two years had the highest relative probability of use. Selection for idle native grasslands increased with age. We also found selection influenced brood success; broods that succeeded were more likely to choose available habitats with more shrub cover, while failed broods avoided available habitats with more shrub cover. Successful broods also selected areas farther from trees than failed broods.

To quantify full annual cycle population dynamics in an integrated population model, we tracked 766 juveniles and 618 adults during the breeding season, we tracked 772 juveniles and 349 adults during the non-breeding season, we monitored success of 276 nests incubated among 576 adults, and conducted whistle counts in May 2016–2018. Talbot Conservation Area had the lowest population growth rate (λ_{TAL} = 0.31, 95% CRI: 0.03, 0.65), due to low fecundity and summer adult survival. Shelton Memorial Conservation Area had low estimated breeding season juvenile survival, non-breeding season survival, and the second lowest population growth rate (λ_{SLT} = 0.37, 95% CRI: 0.00, 0.74), possibly due to its small area (320 acres) and low bobwhite density. Stony Point Prairie had high fecundity and adult breeding season survival probabilities, but the lowest non-breeding season survival among all sites, which depressed population growth

(λ_{STP} = 0.51 95% CRI: 0.08, 0.85). Extensive native grasslands had consistently higher fecundity and adult summer survival probabilities than intensively managed conservation areas. Wah'Kon-Tah Prairie, our largest extensively managed site, had the highest population growth rate ($\lambda_{WKT} =$ 0.55, 95% CRI: 0.13, 0.94). We found declining population trends on all conservation areas. Non-breeding season survival from 1 November to 30 April was most strongly correlated with abundance, followed by juvenile breeding season survival. Greater, less variable non-breeding season survival is required to achieve population stability.

Further evaluation of intra-annual environmental influencers and the relationship between habitat area and population viability would better inform bobwhite management approaches. Important next steps in this research include examining finer temporal scales that separately evaluate breeding, winter, and transitional periods in the annual cycle. Additionally, effects of weather and climate on population viability will be important considerations as Missouri experiences warmer temperatures and potentially extreme changes in precipitation patterns. Finally, this study generated valuable data that can be used to simulate regional population trends and projections across the surrounding landscape.

CHAPTER 1

EFFECTS OF HABITAT MANAGEMENT, WEATHER, AND SEASONALITY ON NORTHERN BOBWHITE JUVENILE BODY CONDITION

ABSTRACT

Precocial young leave their nest immediately after hatch to move and forage as a group during a rapid period of development. Growth and body condition are correlated with survival; young are better able to thermoregulate as they become larger, and they are better able to escape predators as they become more mobile. Environmental conditions can influence development and ultimately survival. We evaluated weather, habitat, and temporal factors affecting northern bobwhite juvenile-body condition. We captured 216 individuals from 33 broods >16-days old on 5 conservation areas in southwest Missouri in 2017 and 2018. Brood hatch dates ranged from 10 June through 19 September. Body condition was measured as the residuals from a linear regression of juvenile tarsus length and body mass on capture. We found some support for improved body condition earlier in the breeding season, under warmer average high and average minimum temperatures, and in native grasslands that were burned and grazed within the previous two years. However, our models representing hypothesis tests were similar to the null model (i.e., ΔWAIC<2), indicating the effects we examined did not explain substantial variation in bobwhite body condition. This may be due to limited data or the influence of other environmental factors not considered in our competing model set. Early breeding season is an important period for successful bobwhite productivity and native grasslands in managed with rotational fire and grazing may create higher quality brood rearing habitat for improved juvenile-body condition.

INTRODUCTION

Body size and condition directly influence mobility and survival of young birds (Rotella and Ratti 1992, Wisdom and Mills 1997, Krapu et al. 2000, Vitz and Rodewald 2011, Anteau et al. 2014, Cox et al. 2014, Jones et al. 2017). Larger precocial chicks are better able to thermoregulate and are more mobile than smaller ones, which may improve foraging efficiency and predator avoidance (Visser and Ricklefs 1995, Schekkerman and Boele 2009). For example, body size of King Eider (*Somateria spectabilis*) ducklings was positively associated with individuals' sprint speed and endurance (Anderson and Alisauskas 2001). Piping Plover (*Charadrius melodus*) chicks that gained weight faster in the first two weeks of life were more likely to survive (LeFer et al. 2008). Thirty-day Spectacled Eider (*Somateria fischeri*) duckling survival was positively correlated with age-adjusted mass (Flint et al. 2006). Understanding environmental drivers of body condition of precocial young provides insight into factors affecting fitness (i.e., survival) and brood success.

The quantity and nutritional quality of food resources for young broods are patchily distributed and can be affected by season, weather, and habitat (Guthery et al. 2002, Le Fer et al. 2008). Variation in growth and body condition of young chicks may reflect variation in food resource abundance and can be used to assess local forage quality and habitat suitability of brood-rearing areas (Le Fer et al. 2008, Flint et al. 2006, Anteau et al. 2014). In contrast, environments with lower food quality or abundance may result in starvation-induced weakness, reduced body mass, and lower chick survival (Loegering and Fraser 1995). Environments with higher food quality or abundance may result in better chick development, advanced mobility, improved foraging success and predator avoidance, and reduced risk of exposure in cold or wet weather (Jones et al. 2017). Environmental conditions that constrain or enhance growth may be an ultimate factor affecting survival of precocial young (Flint et al. 2006).

Northern bobwhite (*Colinus virginianus*, hereafter bobwhite) are a rapidly-declining shrub-obligate species. Bobwhite have low annual survival and rely on high productivity and recruitment to maintain populations. They exhibit a flexible mating system in which both females and males can incubate nests and attend broods as pairs or independently over a relatively long breeding season that allows for multiple nesting attempts (Roseberry and Klimstra 1984, Curtis et al. 1993, Burger et al. 1995).

For bobwhite juveniles, mortality rates remain high until young reach a mass of over 50 g (Lusk et al. 2005). Bobwhite juveniles have high protein requirements for rapid growth. For the first two weeks post-hatch, young consume mainly insects, and then gradually increase the proportion of seeds and plant material in their diet (Hurst 1972). Protein requirements remain elevated until young reach about two-thirds of their adult weight (Nestler et al. 1942). Brood attending adults select environments with higher invertebrate abundance, and brood home range sizes are inversely related to the invertebrate abundance (De Vos and Mueller 1993). Local abundance and availability of insects influences development, body condition, and survival of young (Nestler et al. 1942, Hurst 1972).

Habitat management, weather, and seasonality likely affect the growth and energy budgets of bobwhite chicks. For example, February burns in old-field type habitats every one to two years increase insect abundance and facilitate chick mobility by removing vegetation litter (Hurst 1972). Wet periods early in the breeding season or cold temperatures experienced by late-season broods may reduce foraging time for young birds (Spiers et al. 1985, Carroll et al. 2015). Insight into juvenile physiological responses to environmental conditions and habitat management will enhance our understanding of mechanisms underlying population dynamics (Guthery et al. 2002, Kentie et al. 2013).

Our objective was to assess environmental influences on body condition of dependent juveniles younger than 30-days old. We predicted body condition would be better for individuals hatching earlier in the summer, during warmer, drier periods, and individuals occupying native grasslands disturbed with fire and grazing practices. We predicted body condition would be poorer for individuals hatching later in the summer, during colder, wetter periods, and for individuals occupying agricultural crop fields or idle native grasslands.

METHODS

Study sites

Our study extent included two intensively managed sites, three extensive prairies, and surrounding private lands in southwest Missouri at the eastern edge of the Tallgrass Prairies. Intensively managed public lands (Shawnee Trail and Robert E. Talbot Conservation Areas) included fine-scale management practices such as strip cropping among smaller grassland units (Fig. 1.1A). Our three extensive prairie sites (Shelton Memorial Conservation Area, Stony Point Prairie, and Wah’Kon-Tah Prairie) had larger, more continuous tracts of native grassland habitat (Fig. 1.1B). Grasslands on all public lands in our study area were managed with fire, grazing, or mowing practices. Private lands surrounding public lands were largely agricultural row crop and cool-season grass pastures and hay fields.

Tracking, capture, marking, and measuring young

Bobwhite nests hatched from early June through late September. We tracked adults during the breeding season, monitored nests, and captured young broods from June through October 2017 and 2018. Nests were located from May through September by following radio-collared adults and systematically searching areas in which adults were tracked two or more consecutive days. Nests were monitored at least three times per week during the incubation period and daily around estimated time of hatch. After hatch, we tracked brood attending adults daily and recorded brood identity, date, time of day, and UTMs for each location. We tracked broods to within 10 m or projected their location based on signal strength and triangulation if a brood was on private land or otherwise not accessible. We tracked broods to at least one roost location per week and rotated daytime tracking order. At approximately three weeks old, we captured broods before first light using thermal imaging cameras and the corral technique (Smith et al. 2003, Andes et al. 2012). We marked young with a patagial tag, weighed each individual with a digital scale, and measured tarsus length with calipers.

Habitat and weather covariates

We classified cover type and management practices across our study extent using primarily descriptive maps from wildlife managers and field crews, but also aerial photos from National Agriculture Imagery Program (NAIP; USDA 2016), and cropland data layers (CropScape; USDA 2018). Herbaceous cover was identified as agricultural row crop, idle agricultural fields, native grassland, mixed grassland, or cool-season grasslands. Row crops included corn, soybeans, winter wheat, and sunflower (*Helianthus* spp). Native grasslands were either remnant or reconstructed prairies, or native grass plantings. Common grass species include little bluestem (*Schizachyrium scoparium*), and Indian grass (*Sorghastrum nutans*), common flowering plants included prairie blazing star (*Liatris pycnostachya*), pale purple coneflower (*Echinacea pallida*), and black-eyed susan (*Rudbeckia hirta*), and woody plants included species such as sumac (*Rhus* spp.) and plum (*Prunus* spp.).

Management practices were classified based on a two-year fire and grazing history of each management unit within a Conservation Area. We only evaluated the influence of agricultural row crop and native-grassland management on juvenile-body condition. Idle native grasslands (Nid) were areas not grazed or burned in the previous two years and not mowed within that growing season. Patch-burn grazed grasslands (Npbgr) were areas that had been both burned and grazed at least once in the previous two years. We quantified average percent cover of each habitat type within 50 m of all daily locations from hatch to capture as our habitat predictors of juvenile-body condition (McGarigal et al 2012).

We collected daily temperature and precipitation data from Missouri Mesonet weather stations in Lawrence County for Talbot Conservation Area and Barton County for Shawnee Trail, Shelton, and Stony Point Prairie Conservation Areas. We collected weather data from one MesoWest station in Cedar County for Wah’Kon-Tah Prairie. Temperature variables considered in our analyses included average high and low daily temperatures (°C) and maximum high and low daily temperatures (°C) from hatch to capture for each brood. Precipitation variables included average and maximum daily precipitation (mm) and number of days of precipitation from hatch to capture for each brood.

Statistical Analyses

We used the residuals from a linear regression of juvenile tarsus length and body mass (P<0.01, r^2 = 0.88) as an index of bobwhite juvenile-body condition (Vitz and Rodewald 2011, Jones et al. 2017). Residuals were normally distributed with a mean of 0 and we assumed positive values were indicative of better body condition.

We used a normally-distributed generalized linear mixed model in a Bayesian framework to evaluate effects of temporal and environmental factors on bobwhite juvenile-body condition JBC_{jk}. We included brood identity, B_j, and site, S_k, as random effects for individuals in brood *j* at site *k* in all models to account for intra-brood and site dependence (Eq. 1). We evaluated the influence of hatch date, *H*, as a fixed temporal effect, temperature and precipitation variables as fixed weather effects, and agricultural, idle native grassland, and managed native grassland cover as fixed habitat effects within 11 single-effect models (Table 1.1). We used vague priors for all random and fixed effects. Fixed environmental effects and hyperpriors for mean site effects had a mean of zero and precision of 0.001. Hyperpriors for standard deviation of brood and site effects had a uniform distribution between 0 and 10. We assumed unaccounted for variation ε_i was normally distributed around zero with a uniformly-distributed standard deviation between 0 and 10. Posterior probabilities for all parameters were calculated using vague priors. Our regression estimating the effects of hatch date (*hatch*) on juvenile-body condition JBC_{jk} and can be written mathematically as:

$JBC_{jk} = B_j + S_k + H * hatch$ Eq. 1

$B_j \sim Normal(0, \sigma.B^2)$

$\sigma.B^2 \sim Uniform(0, 10)$

$S_k \sim Normal(\mu.S, \sigma.S^2)$

$\mu.S \sim Normal(0, 0.001)$

$\sigma.S^2 \sim Uniform(0, 10)$

$H \sim Normal(0, 0.001)$

Eleven total fixed effects parameters were considered singly in models identical to eqn. 1 where habitat and weather variables were each evaluated in place of hatch date (Table 1.1).

We first evaluated each of the 11 effects related to season, habitat, and weather in single-parameter models and compared their predictive ability relative to our null model (Table 1.1; Ellison 2004, Hooten and Hobbs 2015). We ranked model performance by calculating Watanabe-Akaike Information Criterion (WAIC) values using the R package loo to interpret effects among competing models (Watanabe 2010, Gelman et al. 2014, Vehtari et al. 2016). We included seasonality and the most supported habitat and weather parameters from the single-effect models in a set of multiple-effects models to quantify whether predictive performance improved. We considered models useful with ΔWAIC scores >2 from the null model. For each effect, we present the posterior mean, 95% credible intervals, and f-values, which are a measure of confidence in positive or negative parameter effects (Arnold 2010, Jones et al. 2017).

RESULTS

We captured and measured body condition of 216 individuals >16-days old from 33 broods on 5 sites in 2017 and 2018. Brood ages ranged from 16- to 24-days old at capture and hatch dates ranged from June 10 through September 19. We did not include capture data for broods whose nests were not monitored and hatch date was unknown.

Single-effect models incorporating average high temperature, hatch date, burned and grazed native grassland cover performed <2 ΔWAIC better than the null model. While we expected precipitation and idle native grassland management would negatively influence body condition, parameters were not well-supported based on their posterior sample distributions and those single-effect models performed worse than the null model. No single- or multiple-effects models performed >2 ΔWAIC better than our null model, suggesting our models incorporating weather, habitat, and temporal effects did not explain substantial variation in bobwhite juvenile-body condition (Table 1.2).

Directions of environmental effects in our top two models aligned with our predictions; hatch date negatively affected juvenile-body condition and percent native grassland habitat and higher temperatures had a positive effect (Fig. 1.2, Table 1.2). From our single-effects models, average high temperature date, average minimum temperature, and maximum high temperature all performed better than the null model, and had at least 85% support for a positive effect on body condition (Table 1.2). Percent agriculture performed only slightly better than the null, and had 88.8% support for a negative influence on body condition (Table 1.2). While we predicted idle native grassland habitat and precipitation would negatively influence juvenile-body condition, models were not supported and thus these effects did not explain substantial variation in body condition.

DISCUSSION

We found some support for positive effects of warmer temperatures, earlier hatch date, and burning and grazing on native grasslands on juvenile bobwhite body condition. There was also weak support for a negative effect of agricultural row crop on juvenile body condition. Poor predictive capacity of our models either suggests data were insufficient or other intrinsic, temporal, or environmental factors are more important contributors to bobwhite chick growth. Yet, we have reason to believe these effects influence bobwhite juvenile-body condition.

Warmer average and minimum temperatures and earlier hatch dates may increase bobwhite juvenile-body condition. This pattern holds in other precocial species such as golden plover (*Pluvialis dominica*), where weight gain was positively associated with warmer temperatures (Pearce-Higgins and Yalden 2002). Bobwhite may benefit from greater food availability as warmer temperatures can increase foraging time or invertebrate prey abundance earlier in the breeding season during warmer July and August conditions (Schekkerman and Boele 2009).

Habitat effects also weakly supported our hypotheses predicting positive effects of native grassland disturbance and negative effects of agricultural row crop on juvenile bobwhite body condition. Patch burn grazing on native grasslands promotes heterogeneity in plant community structure and composition and can lead to concentrated areas of high invertebrate biomass for foraging broods (Engle et al. 2008). We found some support for a negative influence of row crop cover on juvenile-body condition. While brood foraging and growth rates may be lower in croplands, weedy fields may also provide sufficient invertebrate prey (Puckett et al. 1995, Palmer et al. 2001, Doxon and Carroll 2007, Doxon and Carroll 2010, Lohr et al. 2011).

While we found no relationship between precipitation patterns and juvenile-body condition, other studies have found rainfall increased brooding time and decreased foraging time for young chicks (Schekkerman and Boele 2009). Inclement weather can reduce foraging efficiency, body condition, and survival of adults and their young (Sergio 2003, Anctil et al. 2014, Fisher et al. 2015, Terraube et al. 2017). Precocial young, similar to small mammals, are susceptible to hyperthermia in wet and cold conditions (Stoddard 1931:201, Conley and Porter 1986). Wet and cold conditions that limit foraging activity and reduce insect availability may reduce body condition of young during a vulnerable period of rapid growth, ultimately depressing population recruitment (Stoddard 1931:201, Siikamäki 1996, Lusk et al. 2005, Schekkerman and Boele 2009). Longer term data and larger sampling of bobwhite broods may provide greater perspective on the strength of these anticipated relationships between habitat and weather on juvenile body condition.

We did not evaluate pre-hatching condition effects on juvenile growth. In golden plover chicks, mean hatching weight was positively correlated with mean egg volume within a clutch and also positively correlated with weight gain of 2-day old young (Pearce-Higgins and Yalden 2002). While hatching weight may not predict juvenile survival, weight gained in the first few days of life was greater for plover chicks that survived and the heaviest chicks at 2-days old were the most likely to survive (Pearce-Higgins and Yalden 2002). For bobwhite, heavier eggs also produced larger chicks, which may in turn improve juvenile growth (Skewes et al. 1988, Giuliano et al. 1996).

We did not consider factors potentially influencing egg weight and this may be an avenue of future evaluation.

Understanding environmental drivers of bobwhite chick body condition is an important component of brood ecology. Posterior distributions of some of our parameter estimates agreed with our predictions and provide evidence body condition is not totally independent of weather, seasonality, and habitat influencers. Earlier hatch dates and warmer temperatures may increase foraging time and prey abundance, while patch burn grazing on diverse native grasslands may improve foraging efficiency and invertebrate availability. While predation rates are high for precocial chicks, habitat and weather conditions that constrain growth rates may ultimately affect survival of bobwhite young. The influence of growth on juvenile survival and the sensitivity of population growth to this demographic rate make growth an important contributor to recruitment and full annual cycle population dynamics.

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TABLES

Table 1.1. Minimum (Min), average (Mean), and maximum (Max) observed values covariates evaluated in a study of the influence of season, weather, and habitat on northern bobwhite juvenile-body condition in southwest Missouri 2017–2018.

Parameter		Min	Mean	Max
Hatch	Julian date for nest hatch	10-Jun	15-Jul	19-Sep
Ag	Row crop cover (% in 50 m)	0.0	10.2	74.8
Nid	Idle native grass cover (% in 50 m)	0.0	11.4	89.9
Npbgr	Native grass burned and grazed (% in 50 m)	0.0	9.6	97.9
Tlow	Average daily low temperature (°C)	13.6	19.4	22.3
Thigh	Average daily high temperature (°C)	26.6	30.8	34.1
Tmin	Minimum daily low temperature (°C)	6.3	14.9	18.9
Tmax	Maximum daily high temperature (°C)	31.0	34.8	37.8
Pday	Average daily precipitation (mm)	0.3	2.8	6.2
Pmax	Maximum daily precipitation (mm)	0.4	28.4	47.5
Pn	Number of days of precipitation	1.0	5.2	10.0

Table 1.2. Candidate models explaining the relationship of northern bobwhite juvenile-body condition to hatch date, weather, and habitat factors in southwest Missouri 2017–2018 ranked by ranked by Watanabe-Akaike Information Criterion (WAIC). The mean, 2.5 and 97.5% percentiles, and proportion with the same sign as the mean (f) of the posterior distribution are presented for model fixed effects.

Multiple effect models		mean	2.5%	97.5%	f	ΔWAIC	WAIC
1	Hatch	-0.21	-0.37	-0.04	0.99		
	Npbgr	0.13	-0.03	0.30	0.95	0	348.7
2	Thigh	0.20	0.03	0.37	0.99		
	Npbgr	0.14	-0.02	0.30	0.95	0.2	348.9
3	Hatch	-0.16	-0.34	0.03	0.96		
	Thigh	0.13	-0.07	0.32	0.91		
	Npbgr	0.12	-0.03	0.28	0.94	0.7	349.4
4	Hatch	-0.18	-0.37	0.02	0.97		
	Thigh	0.14	-0.06	0.34	0.92	1.0	349.7
Single-effect models							
1	Thigh	0.23	-0.07	0.40	1.00	0.5	349.2
2	Npbgr	0.20	0.02	0.37	0.99	0.6	349.3
3	Hatch	-0.24	-0.40	-0.09	1.00	0.7	349.4
4	Tmin	0.20	0.01	0.37	0.99	1.3	350.0
5	Tmax	0.15	-0.02	0.34	0.96	1.4	350.1
6	Ag	-0.11	-0.28	0.07	0.89	1.5	350.2
7	Null[b]					1.7	350.4

[a] Hatch = hatch date, Npbgr = native grass grazed and burned in the last two years, Thigh = average high temperature, Tmax = maximum high temperature, Tmin = minimum low temperature

[b] Null model includes random effects for site and brood and null model parameters were included in all competing models

FIGURES

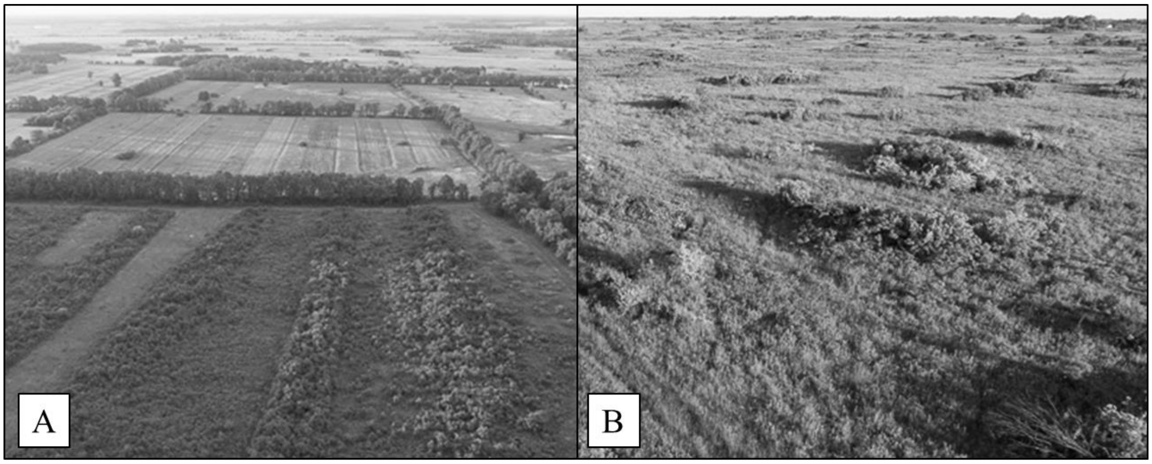

Figure 1.1. Aerial photo of A) Robert E. Talbot Conservation Area, an intensively managed site that applies fine-scale traditional management practices such as fields of strip crop and linear woody vegetation cover for wildlife; and B) Stony Point Prairie, an extensively managed site of native grassland maintained with fire, grazing, and mowing practices in southwest Missouri (photos by David Stonner, MDC 2018).

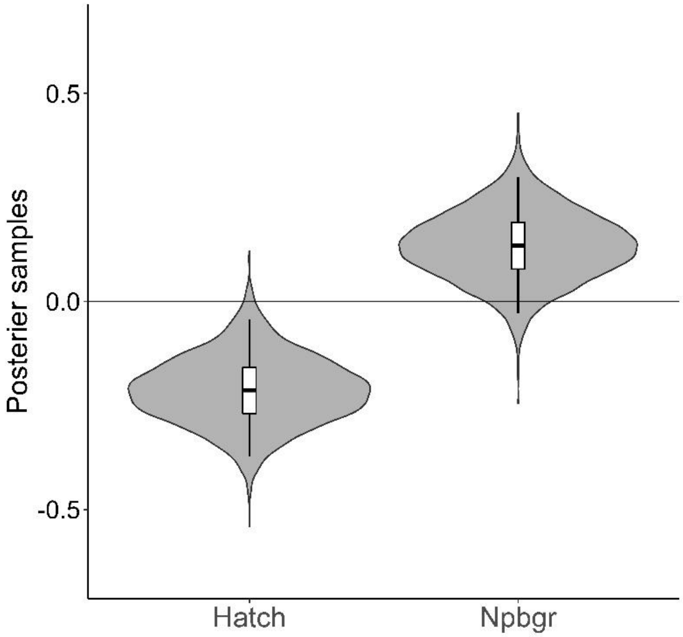

Figure 1.2. Posterior distribution (shaded violin), and 0.05, 0.25, 0.5, 0.75, and 0.975 quantiles (boxplot) for estimated effects of hatch date (Hatch) and percent burned and grazed native grassland cover (Npbgr) on juvenile northern bobwhite body condition in southwest Missouri 2016–2018.

CHAPTER 2

MULTI-SCALE EFFECTS OF LOCAL NATIVE GRASSLANDS MANAGEMENT AND LANDSCAPE COMPOSITION ON NORTHERN BOBWHITE JUVENILE SURVIVAL

ABSTRACT

Effective conservation of declining species requires understanding environmental effects on stage-specific demographic parameters. Local habitat features and landscape context may interactively influence vital rates. Management can structure local habitat features while the degree of isolation or predator community composition are often determined by the surrounding landscape. We determined effects of local habitat (50 m), landscape context (1 km), and management on survival of juvenile northern bobwhite (*Colinus virginianus*) 1- to 100-days old. We monitored daily juvenile survival using radio-telemetry by tracking attending adults from chick hatch to brood capture and then tracking radio-tagged young through a maximum of 114 days. Maps of cover type, management activities, and woody vegetation were used to calculate 50 m and 1 km habitat composition metrics. We estimated survival using a Bayesian known-fate logistic exposure model and tested hypotheses related to effects of age, local habitat management, landscape composition, and woody structure. We evaluated 13 competing models based on ΔWAIC. Survival was greatest in native grasslands that were burned and grazed at least once in the previous two years. Percent shrub cover at the local scale had a nearly credible, positive effect on survival. Percent agriculture at the local scale also had a positive effect on juvenile survival, but an interaction with landscape-level agriculture suggested that small agricultural patches surrounded by non-agriculture negatively affected survival. Patch-burn grazing practices on native grasslands positively influenced bobwhite juvenile survival. Interactive effects of landscape agriculture with managed native grasslands suggest modern mixed landscapes may support juvenile survival and recruitment if appropriately managed native grasslands are available.

INTRODUCTION

The importance of habitat on wildlife population dynamics varies as a function of habitat sensitivity at different life stages, habitat quality and quantity, and associations of neighboring habitats (Kane et al. 2017). Population change is driven by demographic rates of life stages that exert a strong influence on population growth. These life stages may have unique resource requirements or environmental sensitivities. Understanding habitat influences on demographic rates of life stages that regulate population growth can improve conservation and management (Wisdom et al. 2000). Spatial variation in habitat quality and landscape composition influencing sensitive demographic rates may ultimately affect patterns of population extinction or persistence (Moilanen and Hanski 1998).

Northern bobwhite (*Colinus virginianus*; hereafter bobwhite) have experienced long-term, range-wide declines due to suppression of fire on early successional landscapes, agricultural intensification, and sprawling low-density housing development (Brennan 1991; Hunter et al. 2001; Hernandez et al. 2013). Population growth is more sensitive to fecundity than survival for short-lived species with high reproductive potential (Roseberry 1974; Sæther and Bakke 2000; Stahl and Oli 2006; Kane et al.

2017). Annual survival of adult bobwhite in stable populations can average 13%. Thus, juvenile survival and recruitment must compensate for low annual survival to maintain viable populations. There is increasing evidence that juvenile survival and recruitment are strongly correlated with fall abundance and population growth (Roseberry 1974; Williams et al. 2012; McConnell et al. 2018). Bobwhite have a long breeding season (May–September), females can lay large clutches and multiple nests, and both males and females can take on incubation and brood-rearing responsibilities independently or as pairs (Burger et al. 1995). This flexible mating system maximizes reproductive potential yet juvenile survival is often very low.

The first 30 to 35 days post-hatch is a critical survival period for bobwhite (Stoddard 1931; Lusk et al. 2005). Young juveniles lack fully-developed feathers, they are flightless before 14-days old and dependent on adults for thermogenesis before 18-days old, and require high protein diets for rapid growth (Stoddard 1931; Hurst 1972; Spiers et al. 1985; Lusk et al. 2005). Previous studies based on nest monitoring and brood counts estimated survival to be 38% in the first 2—3 weeks of life (De Vos and Mueller 1993; DeMaso et al. 1997). Daily survival of precocial young improve with growth (Stoddard 1931; Pearce-Higgins and Yalden 2002; Lusk et al. 2005). Thirty-day period survival estimates of bobwhite juveniles ≥2 weeks old range from 77.9 to 83.1% (Suchy and Munkel 2000; Tanner et al. 2019). These estimates do not represent the full growing period, which is approximately 145 days from hatch to mean subadult winter weight (Roseberry 1971). Juveniles grow rapidly in the first 74 days of life, from less than 10-g to 149-g, and then steadily up to 180-g at around 145 days (Roseberry 1971). Few survival estimates include the most vulnerable period of life, the first 1 to 3 weeks.

Telemetry-based period estimates start between 8- and 21-days old and end between 34- and 56-days old (De Vos and Mueller 1993; DeMaso et al. 1997; Suchy and Munkel 2000; Lusk et al. 2005; Kamps et al. 2017; Tanner et al. 2019). Longer period estimates may be important for understanding breeding-season patterns of juvenile survival.

Recent long-term studies using joint live and dead encounter models found recruitment and seasonal chick survival is highly variable and influenced by the amount and timing of precipitation during the breeding season (McConnell et al. 2018, Terhune et al. 2019). These studies provide important insight into inter- and intra-seasonal variation in productivity, but there is limited information on juvenile survival responses across heterogeneous habitats and altered landscapes (Gates et al. 2012). Recent telemetry-based studies examining habitat effects on juvenile survival found a positive relationship with indices of habitat suitability and a negative relationship with indices of interspersion of burned, non-burned, and wetland habitats within a brood's home range (Kamps et al. 2017, Tanner et al. 2019). These studies suggest habitat and management-associated variation in juvenile survival, but they are limited to single wildlife management areas and do not address habitat-specific survival at immediate daily brood locations.

Bobwhite broods occupy a variety of habitats within the fragmented eastern tallgrass prairie landscape, including native and non-native grasslands, scrublands, woodlands, and agricultural fields. We hypothesized combinations of cover type (agriculture, native-, mixed-, and cool-season grasslands) and management strategy (burning, grazing, mowing, idle) create unique habitats that differentially affect survival of young. Our objectives were to (1) estimate bobwhite juvenile survival from hatch through 100-days old and (2) determine multi-scale effects of habitat management and landscape composition on this demographic rate.

METHODS

Study site

We studied bobwhite in southwest Missouri on five Missouri Department of Conservation (MDC) conservation areas and surrounding private lands (Fig. 2.1). The region is at the eastern edge of the tallgrass prairies but has been largely converted to non-native pasture and cultivated crop. Nevertheless, this area has a high habitat potential for successful bobwhite habitat management and population recovery (Homer et al. 2011; Morgan et al. 2016). Three of our study sites were extensively-managed remnant prairies that ranged in size from 320 to 3030 acres: Wade and June Shelton Memorial Conservation Area (SLT), Stony Point Prairie Conservation Area (STP), and Wah'Kon-Tah Prairie (WKT). These sites employed combinations of fire, grazing, brush hogging, and haying to maintain the grassland landscape, with limited woodland habitat (<6%). Prescribed burns with grazing and mowing enhance species richness on native tallgrass prairies, mimicking pyric herbivory characteristic of historic disturbance regimes (Collins et al. 1998; Fuhlendorf et al. 2004). By contrast, our two intensively managed sites were Shawnee Trail Conservation Area (SHT) and Robert E. Talbot Conservation Area (TAL), which ranged in area from 3635 to 4361 acres. These sites were a patchwork of smaller management units incorporating agricultural strip crop and woodland habitats 2 to 60 acres in size among larger grassland units. Traditionally-managed areas used prescribed grazing, mowing, and burning of grassland units but also employed fine-scale habitat improvement practices such as planting food plots and maintaining woody-edge cover. These conservation areas are surrounded by mainly private cool-season grass pastures managed for cattle and hay, and corn and soybean fields.

Juvenile capture, marking, and tracking

We estimated bobwhite juvenile survival from hatch to 114-days old from nest monitoring, brood capture, and juvenile tracking data. Brood attending adults were funnel trapped and fitted with radio collars in February and March each year by MDC. All breeding season adults were tracked 3 to 5 times per week from early spring through September to estimate survival and nest success of adults. Nests of radio-tagged adult birds were monitored daily as expected hatch date approached and the number of eggs hatched was recorded. We captured broods for radio-marking and patagial tagging using the corral technique (Smith et al. 2003). Corrals built 1 m tall with a PVC frame and wire mesh window screen were secured around a roosting brood before dawn and a garden net stretched over the corral to prevent adults and young from escaping. Vegetation around the interior edge of the corral was cleared to bare soil to facilitate capture of all individuals after the brood flushed. We used a thermal imaging camera (FLIR E4, FLIR Systems Inc., Wilsonville, OR, USA) to monitor brood activity and help locate all young during capture (Andes et al. 2012). Young were held in animal pet carriers for processing. There is no evidence capture influences survival (Smith et al. 2003; Andes et al. 2012) as individuals are returned to within 10-m of an attending adult immediately after tagging.

Individuals captured at ≤2 weeks of age were uniquely marked with colored permanent marker on their throat, axillaries, and underwing coverts. Juveniles ≥2 weeks of age were marked with numbered aluminum patagial tags (Style 4-1005, Size 1, National Band and Tag Company, Louisvill, KY, USA; Carver et al. 1999) and one to six individuals within each brood weighing over 20-g received 0.6 to 0.8-g radio transmitters using the suture technique (Burkpile et al. 2002; Dreitz et al. 2011, Terhune et al. 2020). Transmitter weight never exceeded 4% of an individual's body mass; 0.6-g transmitters had a 45-day battery life and 0.8-g transmitters had a 60-day battery life (AWE-QC-0.8 and AWE-QC-0.65, American Wildlife Enterprises, Monticello, FL, USA). Transmitters were attached with two sutures placed with 22-gauge needles, tied with 4-0-monofilament, and secured with a surgeon's knot (Terhune et al. 2020). The top suture was tied flush and secure to the juvenile's back, while the lower suture was tied loosely-looped to allow for growth. Transmitters were sutured low on the back and antennae were clipped to approximately 7–cm in length to prevent entanglement in prairie vegetation. Capture and handling protocols were reviewed and approved by the University of Missouri Institutional Animal Care and Use Committee (Protocol 8766).

We tracked brood attending adults from hatch to capture, and then attending adults and radio-tagged juveniles through the life of the birds or the life of their transmitters. We recorded survival status, location, habitat cover type and management, and behavioral observations daily. We tracked broods to roost locations before first light at least once per week and rotated daytime tracking order during the day. We homed in on birds' signals, circled within 10-m of their location, and took care to avoid flushing the group (Orange et al. 2016). If birds were on privately-owned lands that we did not have permission to access we triangulated locations based on azimuths, signal strength, topography and vegetation.

Landscape and habitat covariates

We developed a set of covariates representing combinations of cover type, management history, and vegetation or landscape structure that addressed our hypotheses and were ecologically meaningful for bobwhite survival (Table 2.1). We used field observations, management history information, high-resolution aerial imagery (NAIP 2016; USDA 2016), Cropland Data Layer (CropScape; Han et al. 2012; USDA 2018), and Light Detection and Ranging data (LiDAR; USACE 2015; USACE 2016) to map cover type, management, and woody composition across the full extent of our study area at a 3.6 m resolution.

We calculated focal statistics for class-level metrics of percent cover within a 50 m radius of daily juvenile locations for all local cover type and management combinations and 1 km radius for landscape only cover type in Python (McGarigal et al. 2012). We calculated percent shrub and tree cover at the 50 m and 1 km scales and measured Euclidean distance (m) from locations of individuals to the nearest tree in ArcMap10.4.1 using the Near proximity analysis tool (Table 2.1; ESRI 2019).

We classified herbaceous cover type of management units as native- (N), mixed- (M), or cool-season (C) grasslands, agricultural row crop (Ag), or idle agriculture (Agid) across all conservation area lands, at least 1 km of surrounding private lands, and 1 km surrounding all brood locations. A management unit was a field of a single vegetation community (broadly classified by cover types) and the area at which harvest, fire, grazing, or mowing practices were implemented. Native grasslands included remnant and reconstructed prairies as well as native warm-season grass plantings. Native grassland units were dominated by grasses such as Big Bluestem (*Andropogon gerardii*), Little Bluestem (*Schizachyrium scoparium*), Indian Grass (*Sorghastrum nutans*), Eastern Gamma Grass (*Tripsacum dactyloides*), and have a diversity of forbs such as Leadplant (*Amorpha canescens*), Black-eyed Susan (*Rudbeckia hirta*), Prairie Blazing Star (*Liatris pycnostachya*), Pale Purple Coneflower (*Echinacea pallida*), and Goldenrod (*Solidago* spp.). Remnant prairies were original native grasslands that were never plowed. Reconstructed prairies included units restored from agricultural land use with native Missouri ecotype seed mixes that included 25 to 110 grass and forb species. Ages of reconstructed prairies ranged from 1 to 20 years old. Warm-season grass plantings were established on Talbot in the 1990s from seed originating in Nebraska. Without regular disturbance, these warm-season grass plantings tended to grow thicker and taller than local ecotype seed and had lower forb species diversity. Despite some compositional and structural differences, native grasslands were classified into a single group meaningful for bobwhite, wildlife and landscape ecologists. Cool-season grasses occurred mainly on private lands surrounding our study sites and were dominated by non-native species such as Tall Fescue (*Festuca arundinacea*), Orchard Grass (*Dactylis glomerata*), or Timothy Grass (*Phleum pratense*). Mixed-grassland units included old fields, grasslands composed of both native and non-native grasses listed above or Ragweed plants (*Ambrosia* spp.). Agricultural row crop units included soybean, corn, sunflower, and winter wheat. Idle agricultural units were unplanted or had weedy, failed crops. Water, roads, and buildings in our study area were classified as unusable space.

Management practices were characterized for each management unit by within-season mowing (including haying; mw), a two-year history of fire (pb), grazing (gr), or fire and grazing (patch-burn grazing; pbgr), or idle (id) if units were unmanaged for two consecutive years. Mowing occurred from June to August on prairie reconstruction units on Shawnee Trail for the first two years after planting. Some units on Wah'Kon-Tah were hayed during the summer, though most cutting on prairies occurred from October to November. Private lands were mowed/hayed from June to July. Conservation areas used low-intensity grazing practices consisting of 1 animal unit (454-kg of cattle) per 4–5 acres from April to August (either 90 to 120 days) and grazing units were rested every 1–4 years depending upon grazing management. All areas used to some degree fire with grazing (patch burn grazing) that involved burning 1/3 of a unit annually or biannually with rest periods at the end or after each burn in a burning cycle. Prescribed burns occurred September–April depending upon management objective and were applied every 1–3 years.

We characterized composition of woody vegetation using 2014 LiDAR data from Barton and Vernon Counties and 2016 LiDAR data for Bates, Cedar, Dade, Lawrence, and St. Clair Counties obtained from Missouri Spatial Data Information Services' LAS Download Tool (Hellesen and Matikainen 2013; USACE 2015; USACE 2016). Woody vegetation was classified at 3.6 m resolution across our entire study extent based on the difference between a digital surface model (DSM) and a digital elevation model (DEM); height differences 0 to 0.7-m were classified as ground cover, 0.7 to 3.5-m were classified as shrub cover, and 3.5 to 40-m, tree cover. We corroborated classification using these breaks with ground-truthed GPS waypoints collected across the study area and aerial imagery. Shrubby species composition included Dewberry (*Rubus* spp.), Dogwood (*Cornus* spp.), Sumacs (*Rhus* spp.), and young Oak saplings (*Quercus* spp.).

Hypotheses

We constructed a set of candidate survival models to evaluate the following hypotheses that were based on our understanding of bobwhite brood ecology and predicted effects of age, local habitat cover, landscape context and composition, woody vegetation structure, and bobwhite habitat management strategies.

H0: *Juvenile survival improves with age*. There is existing evidence that survival of young birds improves with age and body size (Lusk et al. 2005; Cox et al. 2014).

H1: *Juvenile survival varies with local cover type and management of habitats that broods occupy*. Resource heterogeneity at the immediate location of an individual may influence survival (Wiens 1989; Dunning et al. 1992). The structural heterogeneity and richness of native and mixed grassland vegetation managed with grazing, burning, or patch-burn grazing will positively influence juvenile survival (Hurst 1972; Kamps et al. 2017). Cool-season pastures and hay fields will negatively influence juvenile survival. Mowing practices and idle grasslands will negatively influence juvenile survival (Perlut et al. 2006; Martin et al. 2015). Agricultural lands will negatively influence juvenile survival (Matson et al. 1997, Benton et al. 2003, Wilson et al. 2005, Askins et al. 2007).

H2: *Juvenile survival varies with landscape composition and landscape context modifies local habitat effects*. Landscape composition may directly influence survival or interact with local resource conditions to influence survival (Wiens 1993; Dunning et al. 1992; Morris 2003; Bloom et al. 2013, Heisler et al. 2017). Increasing proportion of native grasslands at the landscape scale will improve juvenile survival, whereas increasing proportions of agricultural fields and cool-season pastures will negatively influence juvenile survival (Loman 1991; Taylor et al. 1999; Ribic et al. 2009; Fraterrigo et al. 2009; Potter et al. 2011; Kentie et al. 2013). Small areas of suitable habitat may be important for maintaining survival necessary for population stability in altered landscapes (Kane et al. 2017). Islands of native grassland habitat within agricultural or cool-season pasture landscapes will have greater juvenile survival than local agricultural or cool-season grassland habitats within those non-native landscapes.

H3: *Woody composition and configuration at the local and landscape scales influence juvenile survival*. Bobwhite are a shrub-obligate species, so increasing local- and landscape-level shrub cover will positively influence survival by providing broods visual obstruction from avian predators and thermal refugia from high summer temperatures (Roseberry and Sudkamp 1998; Janke et al. 2015; Tanner et al. 2017). Increasing tree cover and proximity to trees will reduce juvenile survival by providing nearby habitat for mesocarnivores and perches for aerial predators. Increasing tree cover at the landscape scale will also reduce the amount of usable space (Veech 2006).

H4: *Juvenile survival is relatively low on private lands, greater on intensively managed quail emphasis areas, and is greatest on extensively managed native grasslands*. Juvenile survival will be highest within Wah'Kon-Tah, Shelton, and Stony Point Conservation areas managed as extensive native prairies with patch-burn grazing (Balent and Norment 2003; Sadoti et al. 2017). Juvenile survival will be higher within our intensively managed sites, Shawnee Trail and Talbot Conservation Areas, than on private lands largely converted to crop fields and cool-season pastures (Kentie et al. 2013).

Survival analysis

We estimated juvenile survival from hatch to 114-days old using nest monitoring, brood capture, and radio-telemetry tracking data. Initial brood sizes were estimated based on the number of hatched eggs counted in a nest within 1 to 2 days after hatching. If broods were discovered with a radio-tagged attending adult and no nest information was available, initial brood sizes were counted from number of chicks on first capture. For early period survival estimates (hatch to approximately 21-days old), individual fates from nest hatch or from counts of initial brood size during young captures (4- to 12-days old) were recorded on final captures (approximately 21-days old). Nest and capture data only contributed to early period survival when (1) young brood sizes were observed from nest monitoring or young brood captures and (2) when brood captures from roost locations were successful and complete. Counts from roost locations are a reliable method for observing early survival of precocial young and reduce some detection error associated with daytime flush counts of cryptic, evasive young (Dahlgren et al. 2010; Schreiber et al. 2016; Kamps et al. 2017). Between hatch and final capture, attending adults were tracked daily and provided habitat information to associate with early period juvenile survival.

Once individual juveniles were fitted with transmitters, survival was estimated through direct daily observation of radio-tagged young. Individuals that died within 3 days of capture were excluded from the analysis under the assumption capture and handling influenced their death (Larson et al. 2001). We right-censored observations for individuals due to transmitter signal loss or unknown fate but included observations up to the last observation of known fate (Tanner et al. 2019).

We estimated multiple effects (j) of age, cover type, management, and woody composition (β_j) on juvenile survival (p_i) for each daily observation (i) using known-fate logistic exposure survival models (Shaffer 2004) in a Bayesian framework (Eq. 1). This method is similar to logistic regression but uses a modified link function that contains interval length (t), which allows time between survival observations (S_i) to vary and estimation of daily survival as an exponential function of t (Shaffer 2004; Shaffer and Thompson 2007). Interval length between hatch and captures averaged 12.2 days (range 1–23 days) and between tracking locations 1.2 days (range 1–13 days). The model's accommodation of variable time lengths between observation intervals allowed for a streamlined estimation of early and late period survival from nest, capture, and tracking data in a single model.

We estimated the mean and variance for a vector of fixed effects including age, cover type, and management activities, β_j, and a common intercept, γ (Eq. 2) in generalized linear mixed models with the modified link function (Eq. 1). All models included a fixed quadratic age effect (days) because survival of young improved with age and body size (Lusk et al. 2005; Cox et al. 2014). We standardized values of age, as well as local and landscape composition to transform variables to mean 0 and units of standard deviation to address differences in variable scale. We calculated the variance inflation factor (VIF) among predictor variables and ensured all variables in a model had a VIF of <2.5 to avoid problems with multicollinearity. We also quantified variance of random effects for site (α_k), year (α_l), and brood identity (α_m) for each subgroup (Eq. 2). All survival models included a random effect for brood identity to account for non-independence of individuals fates within a brood (DeMaso et al. 1997). We also included site and year as random effects in all models to account for non-independence associated with spatial and temporal variation (Terhune et al. 2019). Applying site as a random effect prevented bias in all model parameter estimates and underestimation of the variance (Darrah et al. 2018). Mean random effects were set to zero and precision of random effect parameters were interpreted as variation among a larger sample of broods, years, and sites (Bolker et al. 2009).

$S_{jklmi} \sim bernoulli(p_{jklmi})$ Daily survival distribution

(1)

$p_{jklmi} \sim s_{jklmi}^{t}$ Modified link function

$\log(s_{jklmi}) = \gamma + \beta_j x_i + \alpha_k x_i + \alpha_l x_i + \alpha_m x_i$ Linear predictor function

$\gamma \sim normal(0, 0.0001)$ Intercept distribution (2)

$\beta_j \sim normal(0, 0.0001)$ Fixed effects distributions

$\alpha_k \sim normal(0, \sigma_k^2)$ Random effects distributions

$\sigma_k^2 \sim gamma(0.01, 0.01)$ Precision of random effects

We fit survival models in a Bayesian framework in Program R version 3.6.1 (R Core Development Team 2019) using JAGS (Plummer 2003) via the JagsUI package (Kellner 2019). We specified vague priors for normally-distributed age and habitat parameters with mean 0 and precision 0.0001. We also specified vague hyper priors for precision of random effect parameters, using a gamma distribution with shape and scale parameters of 0.01. We ran models for 20,000 iterations, a burn in of 10,000, and a thin of 4 for a total of 7,500 samples from the joint posterior and considered convergence successful if effective sample size was > 100 and R-hat < 1.100 (Brooks and Gelman 1998). We increased the number of iterations and adjusted the burn in as necessary if needed to achieve model convergence.

We developed 13 candidate models based on our four hypotheses and a null model that contained random effects for site, year, and brood and a fixed age effect (Table 2.2). We formulated multiple models for some hypotheses to represent multiple levels of complexity and some models represented multiple hypotheses. To evaluate H1, we included a management-only, cover type-only, and two cover type-management models with additional terms for local woody composition or cool season grasslands. To evaluate H2, we included four models that looked at independent effects of 1-km agricultural, native grassland, and cool-season grassland composition and their interactive effects with local agricultural and native grassland cover. To evaluate H3, we included a model with woody-only terms for local and landscape shrub and tree composition and configuration, we also included local shrub cover and distance to tree in some H1 models, and landscape tree cover in one H2 model. To evaluate H4, we included a site model with fixed effects for each of our five conservation areas and a private lands category and a broad management model comparing survival on intensively managed sites, extensively managed sites, and private lands.

We evaluated model convergence by checking for Rhat test statistic values of <1.1 for all model parameters (Gelman and Hill 2007, Kéry and Schaub 2012). We also inspected trace plots to check that Markov chains were well-mixed (Link and Barker 2010, Kéry and Schaub 2012). We evaluated support for our hypotheses by ranking models based on WAIC, interpreted results for models with ΔWAIC < 6 from our top model, and focused our interpretation on effects with 95% credible intervals (CRI) that did not overlap zero (Beauchesne et al. 2013).

RESULTS

We monitored survival of 705 individuals from 75 broods across 5 sites (SHT = 10, SLT = 10, STP = 17, TAL = 15, WKT = 23), 2016–2018, for a total of 14,904 exposure days. This included 493 individuals observed from hatch to young capture (~12-days old) and/or older brood capture (~21-days old), and 212 radio-tagged individuals. We captured 23 young broods 5- to 16-days old and 62 old broods 17- to 29-days old and determined there were 261 mortalities from hatch to capture. We monitored 212 radio-tagged individuals up to 114-days old and observed 64 mortalities. We censored 54 individuals due to dropped collars (mean age = 28 days, range 16–56), 27 due to lost signal (mean age = 37, range 18–58), 3 individuals on private lands whose fate could not be determined, and 3 individuals with transmitter-related mortalities. Sixty juveniles from

31 broods contributed to survival estimates from 61- to 86-days old, and 22 juveniles from 10 broods contributed to estimates from 87- to 114-days old.

We found greater support for our null model with a quadratic versus linear effect of age based on a lower WAIC score (ΔWAIC = 0.56). Therefore, all competing cover type, management, and landscape models included this quadratic age effect. Daily survival increased non-linearly from 96.6% post-hatch to >99.9% at 114-days old (Fig. 2.2). From this age-based model, we estimated 28.6% (95% CI: 0.15, 0.41) 114-day period juvenile survival within our study area.

Six of our eleven competing models performed better than the null model. These six models addressed H1 and H2 expectations of local cover type and management effects on survival as well as their interactive effects with landscape-level agricultural composition (Table 2.2). Models addressing H3 and H4 supported effects of site, private-intensive-extensive management strategies, woody composition, or landscape-level cool-season and native grasslands cover on juvenile survival (Table 2.2). We interpreted the top four models which had at least one credible effect and ΔWAIC <6 units from the top model.

Our top two models addressed H1 and evaluated the effects of local cover type and management combinations on juvenile survival (Table 2.2). Both showed native grasslands burned and grazed (Npbgr) in the past two years had the largest positive effect on daily juvenile survival (Fig. 2.3, Table 2.3). One-hundred and fourteen-day period survival increased from 0.24 (95% CRI: 0.08, 0.41) to 0.84 (95% CRI: 0.56, 0.94) over a range of 0–100% native grasslands burned and grazed (Fig. 4). Both top models also had a positive effect of grazed mixed grasslands (Mgr) on daily survival (Fig. 2.3, Table 2.3) and period survival increased from 0.34 (95% CRI: 0.18, 0.48) to 0.84 (95% CRI: 0.37, 0.97) over 0–100% cover (Fig. 2.4). Effects of local agriculture (Ag) were positive and credible in our second-ranked model (Fig. 2.3, Table 2.3) and period survival increased 0.30 (95% CRI: 0.13, 0.46) to 0.71 (95% CRI: 0.37, 0.89) over 0–100% cover (Fig. 2.4). Local mixed grass prescribed burned (Mpb) had >0.90 of the posterior distribution below zero (f-value > 0.91) but the 95% credible interval overlapped zero (Fig. 2.3, Table 2.3); period survival decreased from 0.40 (95% CRI: 0.22, 0.53) to 0.04 (95% CRI: 0.00, 0.50) over 0–100% cover (Fig. 2.4). The 95% credible interval for shrub cover overlapped zero but 0.925 of the posterior distribution was positive and survival increased 0.31 (95% CRI: 0.13, 0.48) to 0.78 (95% CRI: 0.18, 0.97) over 0–52.5% cover ($f = 0.925$; Table 3, Fig. 2.3, 2.4).

Our third ranked model (ΔWAIC = 1.87) addressed interactive effects of local native grassland and agricultural cover with landscape-level agriculture composition and indicated mixed support for H3 (Table 2.2, Fig. 2.5.). Ninety-five percent credible intervals for local- and landscape-level agricultural effects did not overlap zero (Table 2.3). Positive effects of local native grassland cover were nearly credible and the interactions between local cover types and percent agriculture within a 1-km radius were credible and indicated agricultural composition in the surrounding landscape influenced the effects of local native grassland and agricultural cover on juvenile survival (Table 2.3, Fig. 2.5). While the full range of landscape-level agriculture represented in the data was 0–92.7% cover within 1-km, we report period survival from 0–46.3% cover here because 95% of our observations lie within this range. When local native grassland cover equaled zero, juvenile period survival decreased with increasing landscape-level agricultural cover from 0.38 (95% CRI: 0.11, 0.64) to 0.01 (95% CRI: 0.00, 0.25) for local native grasslands and for local agriculture (Fig. 2.5.A.). When local agriculture equaled zero and native grass was held at its mean, 41.3%, survival decreased with increasing agriculture from 0.41 (95% CRI: 0.16, 0.63) to 0.04 (95% CRI: 0.00, 0.33) as landscape agriculture increased (Fig. 2.5.D.). When local agricultural cover equaled 100% and native grass cover equaled 0%, juvenile period survival increased with increasing landscape-level agriculture from 0.09 (95% CRI: 0.00, 0.60) to 0.62 (95% CRI: 0.17, 0.90; Fig. 2.5.F.). When local native grassland cover equaled 0% and local agriculture was held at its mean, survival decreased with increasing agriculture from 0.38 (95% CRI: 0.11, 0.64) to 0.01 (95% CRI: 0.00, 0.25; Fig. 2.5.B.). When local native grassland cover equaled 100% and local agriculture equaled 0%, landscape-level agricultural composition did not explain substantial variation in juvenile survival; period estimates ranged from 0.36 (95% CRI: 0.11, 0.62)–0.39 (95% CRI: 0.04, 0.74; Fig. 2.5.C.). Our results do not support effects of landscape-level grasslands cover or their interactive effects with local cover type (H2; Table 2.2).

Our fourth ranked model evaluated effects of agricultural and grasslands management on conservation area units and indicated additional support for H1 (ΔWAIC = 3.71; Table 2.2). Similar to previous models, patch-burn grazing, grazing, and row crop agriculture, practices all positively influenced survival (Table 2.3) and 114-day period survival increased to 0.75, 0.67, and 0.61 at 100% cover type, respectively. While our management model (4th ranked) was competitive, our model evaluating cover type effects alone was not supported (11th and 12th-ranked model, Table 2.2). We also did not find support for a difference in survival across sites (8th-ranked model) or across private lands, intensively managed sites or extensively managed native sites (9th-ranked model, Table 2.2).

DISCUSSION

We estimated juvenile survival from hatch to 114-days old across a variety of cover types occupied by broods, including idle and planted agricultural fields, woodlands, and grasslands managed with fire, grazing, and mowing. We demonstrated the importance of including early-period, post-hatch observations into survival estimates for precocial young and found that local habitat management and landscape context affected survival of this vulnerable life stage. Habitat structure and composition that optimize brood period survival may be unique from nesting period resource requirements for juvenile growth, mobility, and cover (Brooke et al. 2017, Jenkins et al. 2017a; Jenkins et al. 2017b; Tanner et al. 2019).

Development and survival of precocial young

Period survival for 1- to 114-days old was 28.6% (95% CRI: 0.15, 0.41). Bobwhite young are 92% of their full body size at 114-days old (Roseberry and Klimstra 1971). Survival of precocial young improved with age and growth as birds developed and gained mobility and independence, therefore it is important to estimate juvenile survival through the full growing period (Lusk et al. 2005; Kentie et al. 2013). We used nest, capture, and juvenile tracking data to estimate a longer period survival incorporating more of the developmental stage of young than previous studies (De Vos and Mueller 1993; Suchy and Munkel 2000; Tanner et al. 2019).

Our early-period survival estimates included uncertainty associated with detectability of individuals and brood adoption, amalgamation, and abandonment. While young are cryptic and may freeze, run, or fly in response to threats, capturing broods on roost sights reduces error in brood counts (DeMaso et al. 1997; De Vos and Mueller 1993; Suchy and Munkel 2000; Dahlgren et al. 2010). Brood adoption, amalgamation, and abandonment are rare early in the brood stage while juveniles are vulnerable and dependent and most brood switching occurs after 14- to 21-days old (De Vos and Mueller 1993; Suchy and Munkel 2000; Faircloth et al. 2005). Floating behavior may be costly for single juveniles if brood cohesion contributes to successful recruitment and reduces predation risk (Ridley et al. 2008; Gamero and Kappeler 2015). We did not include individuals suspected of being adopted in brood counts and early period survival estimates. We censored a total of 20 juveniles from our early period survival analyses because individuals were unmarked from a young capture or their size was unusual for their brood age. However, we could not account for juveniles that may have switched out of broods. Hence, our early period survival estimates may be biased low. Brood abandonment by adults may result in low survival estimates if abandonment is interpreted as brood failure. However, brood abandonment tends to occur at 21- to 42-days old, after broods have survived the critical early growth period and after our brood capture window (Burger 1993). We observed females abandoning broods after 32-days old, but these broods often remained with attending males. To avoid misclassifying brood abandonment as brood failure, early-period brood failures were only included in survival estimates when untagged adults were not observed attending broods.

Local cover and management

Juvenile survival was greatest in native grasslands that were both burned and grazed at least once in the past two years. Depredation was the major source of mortality among our radio-tagged young. Burning and grazing disturbances likely improved survival by exposing bare ground, allowing movement and facilitating escape from predators, while also maintaining vegetation height for cover. These disturbances may also improve juvenile-body condition in the first 3 weeks of life, thereby reducing mortalities due to starvation or exposure (Chapter 1). Burning grasslands removes accumulated litter and increases insect abundance, which facilitates foraging efficiency, thereby increasing development and survival of young (Hurst 1972; Nestler et al. 1942; De Vos and Mueller 1993; Taylor et al. 1999; Brennan et al 2000; Burke et al. 2008; Doxon and Carroll 2010; Gruchy and Harper 2014; Kamps et al. 2017). Attending adults preferentially selected diurnal habitats with more bare ground, greater forb cover, and taller vegetation with greater visual obstruction for young broods (Taylor et al. 1999). For roost habitat, attending adults select locations with tall vegetation and litter deeper than diurnal habitat (Taylor et al. 1999). The spatial juxtaposition of small, frequent fires may optimize food abundance and foraging efficiency within diurnal habitat and create suitable roost sites with greater litter depth in close proximity (Taylor et al. 1993; Taylor 1999; Knight and Holt 2005; Kamps et al. 2017). Fire on native grasslands had a positive influence on juvenile survival across our study area, but fire on mixed grasslands had a negative influence. We had no a priori expectation on effects of fire on mixed grasslands. This cover type is variable across our study extent and includes old fields, native grass plantings invaded by Sericea Lespedeza (*Lespedeza cuneata*), and other herbaceous cover not dominated by native grasses or tall fescue. Furthermore, sites that had burned in previous 12 months had lower survival for bobwhites from November through January than sites that had not burned that recently on our study areas (Mosloff 2020), demonstrating the seasonality of some of these relationships.

We found grazing on mixed and native grasslands increased bobwhite juvenile survival. In addition to fire, grazing can open ground-level grassland vegetation while maintaining adequate height for nesting and brood-rearing activities (Harper et al. 2015). Although intensive grazing may reduce productivity by removing herbaceous cover and exposing nests and young to predators, light to moderate rotational grazing practices can produce suitable breeding habitat for bobwhite and other grassland birds (Sutter and Ritchison 2005; Perlut et al. 2006; Askins et al. 2007; Harper et al. 2015). Without periodic disturbance, idle native grasslands may grow too dense for bobwhite broods (Gruchy and Harper 2014; Harper et al. 2015). Patch-burn grazing management mimics pre-settlement disturbance, and increases grassland plant species and structural diversity (Fuhlendorf and Engle 2001; Fuhlendorf and Engle 2004).

We hypothesized mowing/haying would negatively influence survival of young, but we found little support for this effect. Native warm-season grasses are harvested later in the year than cool-season hayfields and conservation areas typically mow after nesting season to avoid disrupting breeding activities (Harper et al. 2007; Giocomo et al. 2008; Birckhead et al. 2014). We observed two juvenile mortalities caused by mowing on adjacent private lands. Earlier haying of cool-season grasses tends to overlap more with first nesting efforts for grassland birds (Giuliano and Daves 2002; Harper et al. 2007; Birckhead et al. 2014). Frequent and early summer cutting can cause direct mortality for eggs, nestlings, and fledglings of grassland birds, can lead to higher rates of abandonment and depredation, and delay renesting attempts, significantly reducing fledgling production (Bollinger et al. 1990; Perlut et al. 2006). While late mowing practices had no credible effect on juvenile survival on our conservation areas, other studies have found early mowing or haying can dramatically reduce productivity and contribute significantly to grassland bird declines (Bollinger et al. 1990; Dale et al. 1997; Giuliano and Daves 2002; Perlut et al. 2006; Schekkerman et al. 2008; Luscier and Thompson 2009; Birckhead et al. 2014). Mowing does not improve native grassland composition or structure by increasing plant diversity, opening ground-level vegetation or reducing litter depth and cover (McCoy et al. 2001; Gruchy and Harper 2014).

While bobwhite are a shrub-obligate species, composition and structure of woody vegetation within grassland habitats did not strongly influence juvenile survival. We found a nearly credible positive relationship between juvenile survival and percent shrub cover within 50 m of an individual. Shrubs provide bobwhite broods important thermal cover during peak daytime summer temperatures (Carroll et al. 2015) and proximity to shrub cover positively affected survival of bobwhites on our sites November-January (Mosloff 2020). We expected to find a negative relationship between juvenile survival and proximity to trees and percent tree cover as trees provide habitat and perches that may result in increased predator density or activity (Dinkins et al. 2012), but we did not detect a credible relationship.

Populations of many farmland-associated bird species are declining due to direct or indirect effects of habitat loss and fragmentation, harvest practices, pesticide toxicity, changes in food supply, or changes in predator-prey dynamics (Wilson et al. 2005;

Stanton et al. 2018). We expected agriculture to negatively influence bobwhite juvenile survival as cropland monocultures may provide poor foraging habitat, expose young to rainfall and temperature extremes, and increase harvest-related mortality risk (Wilson et al. 2005). We actually found juvenile survival was positively related to local agricultural row crop cover. Broods readily occupied fields of soybeans, corn, wheat, and sunflower on strip crop units of public lands and surrounding private crop fields during the breeding season before harvest.

Local cool-season grasslands did not have a credible effect on bobwhite juvenile survival across our study area. While we did not detect demographic effects, resource selection results suggest broods avoid cool-season pastures and hayfields (E. A. Sinnott, unpublished data). Non-native grasses can influence mobility and raise thermal stress of bobwhite young (Martin et al. 2015). Tall fescue-dominated grasslands and monocultures have dense vegetation, lack bare ground, and have low plant species diversity, creating poor habitat for brood foraging and movement (Stoddard 1931; Barnes et al. 1995; Washburn 2000).

We found site and management regime did not explain variation in bobwhite juvenile survival. We expected survival to be higher on extensively managed sites, such as Wah’Kon-Tah and Stony Point, compared to intensively managed sites, such as Talbot and Shawnee Trail. We suspect we did not find support for these hypotheses because survival was best explained by local habitat features and a combination of herbaceous cover type and management. We also expected survival to be higher on those publicly managed conservation areas compared to surrounding private, agricultural lands. Very few broods monitored used private lands exclusively and so many of our daily survival observations on private lands came from broods that spent a significant amount of time on public lands. Characterizations of sites and management regimes did not capture fine-scale variation in vegetation structure and composition important for broods (Taylor et al. 1999; Tanner et al. 2019).

Landscape composition and local habitat interactions

We evaluated interactive effects of cover at local (50 m) and landscape (1 km) scales on juvenile survival because we hypothesized spatial associations between local habitat used and landscape context influence survival (Kane et al. 2017). We expected landscape-level native grassland composition to positively influence survival because abundance and population growth for bobwhite and other grassland obligate species are positively associated with larger grasslands (Veech 2006; Ribic et al. 2009; Sadoti et al. 2017). However, we found no support for landscape effects of proportion native and non-native grassland cover or their interactions with local native grassland and agricultural cover on bobwhite juvenile survival. There was support for an interactive effect between landscape-level agricultural cover and local native grassland and agricultural cover.

Previous studies reported bobwhite populations respond positively to heterogeneous landscapes with mixed grassland, row crop, and woody edge cover composition (Roseberry and Sudkamp 1998; Veech 2006). Research in southern Illinois found a quadratic relationship between bobwhite abundance and percent row crop agriculture at the county level, with greatest abundance observed between 30 and 70% agricultural cover (Roseberry and Sudkamp 1998). A rangewide analysis found increasing bobwhite populations occurred on landscapes with an average of 37.8%

agriculture, and populations with greater than average abundance occupied landscapes that were on average 24.8% agriculture (Veech 2006). The effects of local and landscape-level agricultural composition on bobwhite juvenile survival provide demographic insight into bobwhite population persistence on mixed landscapes.

We detected credible interactive effects between percent crop cover at the 1-km scale and local agricultural and native grassland cover on bobwhite juvenile survival. In local non-native grassland, non-agricultural cover, juvenile survival decreased with increasing row crop cover at the 1-km scale. Broods occupying non-native grassland or wooded field edges in largely agricultural landscapes may be experiencing greater predator pressure in small habitat patches (Loman 1991; Puckett et al. 1995; Hannon and Martin 2006). Juvenile survival in local native grassland cover was insensitive to percent landscape agricultural composition. Small native grasslands may provide important habitat islands for brood success. Juvenile survival in local agricultural habitat was relatively low when the surrounding landscape was non-agricultural cover. This suggests isolated agricultural units, like strip crops, may not benefit juvenile survival. By contrast, brood survival was highest in local agricultural habitat surrounded by a greater proportion of row crops. Row crop agricultural cover may afford broods better visibility of oncoming predators, easier movement across bare ground, overhead cover from crop plants, and distance from predators that inhabit or perch on field border fencerows and trees. At large spatial scales, predators aggregate in areas of greater prey density. At fine spatial scales, distributions of predators and prey may be negatively correlated through predator avoidance behaviors (Dinkins et al. 2012, De Cesare et al. 2014, Ringleman et al. 2018). These predator-prey behavioral dynamics may partially explain interactive effects of landscape-scale agricultural composition and local habitat cover on bobwhite juvenile survival.

Conservation applications for working landscapes

Southwest Missouri is a mixed landscape of largely private pastures and crop fields, with a few, small remnant prairies. We found broods readily used crop fields, but also require nearby shrub cover and appropriately managed grassland habitat (Riddle et al. 2017, Chapter 3). The competing economic realities of private working lands are a long-standing crux in conservation of early successional habitats (Klimstra 1982).

As a species that responds positively to heterogeneous landscapes, there are opportunities to achieve bobwhite population persistence on managed conservation areas and private working lands. Bobwhite population growth rate is sensitive to productivity and recruitment (Folk et al. 2007; Gates et al. 2012; McConnell et al. 2018). Bobwhite populations on landscapes with more native grassland cover hatch more young per adult female (Chapter 4). We found juvenile survival was positively influenced by patch-burn grazing practices on native grasslands and juvenile survival was relatively stable in local native grassland cover as proportion of landscape agricultural row crop increased up to 46%. Strips of native herbaceous vegetation surrounding row crop fields can increase nest incubation rates and summer bobwhite abundance in agricultural landscapes (Palmer et al. 2005; Riddle et al. 2017). Incorporating native grassland cover within a matrix of private working lands may improve recruitment to fall populations. Patches of native herbaceous and shrubby cover can improve bobwhite recruitment and land health and performance.

State and federal conservation programs have promoted establishment of native warm season grasses to stem grassland bird declines while keeping agricultural production economically viable (Washburn et al. 2000; Brennan and Kuvlesky 2005; Harper et al. 2015; Burger et al. 2019). Native warm-season grasses can produce more forage during hot summer months, during droughts, and on marginal lands compared to cool-season grasses in livestock production operations (Harper et al. 2007; Lowe et al. 2016). Native prairie filter strips in annual row-crop systems can reduce runoff (Hernandez-Santana et al. 2013). Adding biological diversity in agricultural systems with native prairie strips can improve system resilience to pests, extreme weather, nutrient, soil, and water loss (Liebman and Schulte-Moore 2015). Recent advances in agricultural production and precision agricultural technology enable modifications to farmland management that could positively influence bobwhite and many farmland bird populations (Riddle et al. 2017; Stanton et al. 2018; McConnell 2019). Bobwhite populations may benefit from these practices via improved juvenile survival and recruitment rates.

Understanding factors affecting survival is especially important for life stages contributing disproportionately to population growth for declining species. For bobwhite, the brood phase is a vulnerable period of development and we found survival during this stage was explained by variation in local habitat composition, structure, and the amount of surrounding agricultural land. Native grasslands that were burned or grazed improved survival and broods using agricultural crop fields had relatively high survival compared to our expectations. Disturbed native grasslands provide rich invertebrate prey resources, facilitate movement along the ground, and create heterogeneous habitat structure and composition for loafing, foraging, and roosting periods. Crop fields can provide adequate foraging habitat in weedy fields or along field borders and young may be better able to avoid predators. Additional research evaluating habitat-specific nest survival and brood resource selection will further improve our understanding of regional patterns in population productivity.

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TABLES

Table 2.1. Description of cover type, management, and site variables included as fixed and random effects in survival models for northern bobwhite juveniles in southwest Missouri 2016 –2018.

Parameters	min	median	Mean	max	Description
Gr	0.00	0.00	0.07	1.00	Mixed and native grasslands grazed at least once in the past two years
Pb	0.00	0.00	0.16	1.00	Mixed and native grasslands burned at least once in the past two years
Pbgr	0.00	0.00	0.17	1.00	Mixed and native grasslands burned and Grazed in the past two years
Mw	0.00	0.00	0.04	1.00	Mixed and native grasslands mowed in current year
Id	0.00	0.00	0.12	1.00	Mixed and native grasslands idle for at least the past two years
Ag	0.00	0.00	0.17	1.00	Agriculture; includes corn, soy, wheat, sunflower
Agid	0.00	0.00	0.03	1.00	Idle agricultural fields
Ng	0.00	0.32	0.41	1.00	Native grassland; includes remnant prairies, native grass plantings, and restored prairies
Ngr	0.00	0.00	0.05	1.00	Native grassland grazed only in the past two years
Npb	0.00	0.00	0.11	1.00	Native grassland burned only in the last two years
Npbgr	0.00	0.00	0.16	1.00	Native grassland burned and grazed in the last two years
Nmw	0.00	0.00	0.02	1.00	Native grassland mowed in the current year
Nid	0.00	0.00	0.08	1.00	Native grassland idle for at least the past two years
Mgr	0.00	0.00	0.03	1.00	Mixed grassland grazed in the last two years
Mpb	0.00	0.00	0.05	1.00	Mixed grassland burned in the last two years
Mpbgr	0.00	0.00	0.01	1.00	Mixed grassland grazed and burned in the last two years
Mmw	0.00	0.00	0.01	1.00	Mixed grassland mowed in current year
Mid	0.00	0.00	0.04	1.00	Mixed grassland idle for at least the past two years
Ag1k	0.00	0.12	0.16	0.93	Percent agriculture (1 km)
Cg1k	0.00	0.19	0.21	0.60	Percent cool-season grassland (1 km)
Ng1k	0.00	0.36	0.36	0.84	Percent native grassland (1 km)
NgAg1k	.	.	.	.	Interaction between percent agriculture at 1 km and native grassland cover at 50 m
AgAg1k	.	.	.	.	Interaction between percent agriculture at 1 km and percent agriculture cover at 50 m
Sh	0.00	0.03	0.06	0.53	Shrub cover
Tr	0.00	0.02	0.09	0.95	Tree cover
TrD	0.00	29.5	59.1	550.8	Distance to nearest tree (m)
Sh1k	0.00	0.03	0.03	0.08	Shrub cover
Tr1k	0.01	0.09	0.10	0.39	Tree cover

Table 2.1 continued. Description of cover type, management, and site variables included as fixed and random effects in survival models for northern bobwhite juveniles in southwest Missouri 2016 –2018.

Parameters	min	median	mean	max	Description
Pri	.	.	.	n=1593	Private lands surrounding conservation areas; typically cool-season pastures and row crops, but also a small remnant prairie and some mixed grasslands
Int	.	.	.	n=1979	Traditionally managed conservation areas; Shawnee Trail CA and Robert E. Talbot CA
Ext	.	.	.	n=1774	Extensively managed native grassland Conservation Areas; Shelton Memorial CA, Stony Point CA, Wah'Kon-Tah Prairie
SHT	.	.	.	n=846	Shawnee Trail Conservation Area
SLT	.	.	.	n=938	Shelton Memorial Conservation Area
STP	.	.	.	n=1207	Stony Point Prairie Conservation Area
TAL	.	.	.	n=1479	Talbot Conservation Area
WKT	.	.	.	n=876	Wah'Kon-Tah Prairie
age	4	35	39	114	Brood age (days)
α	.	.	.	.	Model intercept
s	.	.	.	.	Site random effect
b	.	.	.	.	Brood random effect
y	.	.	.	.	Year random effect

Table 2.2. Competing survival models and associated hypotheses examining the influence of local cover type and management, shrub and tree composition, and landscape cover parameters on bobwhite juvenile survival in southwest Missouri. Parameters are defined in Table 1. Model performance was evaluated using Watanabe-Akaike Information Criterion (WAIC) and models were ranked by ΔWAIC values.

Rank	ΔWAIC	WAIC	[a]Parameters	[b]Hypotheses
1	0	1406.654	Nid + Ngr + Npb + Npbgr + Mid + Mpb + Mpbgr + Mmw + Mgr + Ag + Agid + Cgr + Cgrha + Cha	H1
2	0.752	1407.406	Nid + Ngr + Npb + Ngrpb + Mid + Mpb + Mpbgr + Mmw + Mgr + Ag + Agid + Sh + TrD	H1, H3
3	1.87	1408.524	Ng + Ag + Ag1k + NgAg1k + AgAg1k	H2
4	3.71	1410.364	Id + Gr + Pb + Grpb + Mw + Ag + Agid	H1
5	6.335	1412.989	Ag + Ng + Cg1k + NgCg1k + NgCg1k	H2
6	8.67	1415.324	Ag1k + Ng1k + Cg1k	H2
7	9.371	1416.025	Null	H0
8	9.426	1416.080	P + SHT + SLT + STP + TAL + WKT	H4
9	11.308	1417.962	P + Int + Ext	H4
10	11.396	1418.050	Ng + Ag + Ng1k + NgNg1k + AgNg1k	H2
11	12.737	1419.391	Ag + Ng + Mg + Sh + TrD	H1, H3
12	13.103	1419.757	Cg + Ng + Mg + Sh + TrD	H1, H3
13	15.336	1421.99	Sh + Tr + Sh1k + Tr1k + TrD	H3

[a] All models include an intercept, a quadratic fixed age effect and random effects for brood identity and year; models 1–7 and 10–13 include a random site effect; models 8 and 9 include site as a fixed effect

[b] *Hypotheses:* daily survival are influenced by local native grassland$^+$ and agricultural $^-$cover as well as burning$^+$, grazing$^+$, mowing$^-$, and idle–management prescriptions (H1), interactions between local cover and landscape composition (H2), shrub$^+$ and tree$^-$ composition (H3), and site-scale intensive$^-$ and extensive$^+$ management strategies (H4)

Table 2.3. Effects of local and landscape cover type, management, woody structure, and age on juvenile northern bobwhite survival in southwest Missouri 2016–2018 including mean, 95% credible interval, and proportion with the same sign as mean (f) of posterior distribution for fixed effects, intercepts, and precision of random effects from models with ΔWAIC <6.

	Model 1				Model 2				Model 3				Model 4			
	mean	0.025	0.975	f	mean	0.025	0.975	f	mean	0.025	0.975	f	mean	0.025	0.975	f
Ng									0.24	-0.07	0.56	0.94				
Nid	-0.01	-0.28	0.26	0.53	-0.03	-0.25	0.22	0.60								
Ngr	0.15	-0.09	0.38	0.89	0.15	-0.07	0.36	0.92								
Npb	0.27	-0.12	0.65	0.91	0.27	-0.09	0.62	0.94								
Npbgr	0.69	0.25	1.16	1.00	0.70	0.32	1.11	1.00								
Mid	0.18	-0.23	0.66	0.79	0.15	-0.23	0.60	0.76								
Mgr	0.23	0.01	0.46	0.98	0.23	0.03	0.43	0.99								
Mpb	-0.21	-0.52	0.10	0.91	-0.23	-0.51	0.05	0.94								
Mpbgr	0.03	-0.17	0.26	0.61	0.04	-0.15	0.26	0.65								
Mmw	0.17	-0.06	0.43	0.91	0.16	-0.06	0.41	0.92								
Ag	0.37	-0.02	0.77	0.97	0.40	0.04	0.77	0.99	0.07	-0.29	0.44	0.64	0.32	-0.04	0.68	0.96
Agid	0.05	-0.18	0.29	0.67	0.08	-0.14	0.29	0.77					0.06	-0.15	0.28	0.71
Cgr	0.15	-0.18	0.50	0.80												
Cha	-0.08	-0.31	0.17	0.75												
Cgrha	0.01	-0.20	0.23	0.52												
Sh					0.21	-0.08	0.51	0.93								
TrD					0.07	-0.28	0.42	0.66								
Ag1k									-0.25	-0.72	0.23	0.85				
Ng50m x Ag1k									0.38	0.01	0.76	0.98				
Ag 50m x Ag1k									0.47	0.12	0.83	1.00				

See Table 1 for descriptions; See Table 2 for model performance and rankings.

FIGURES

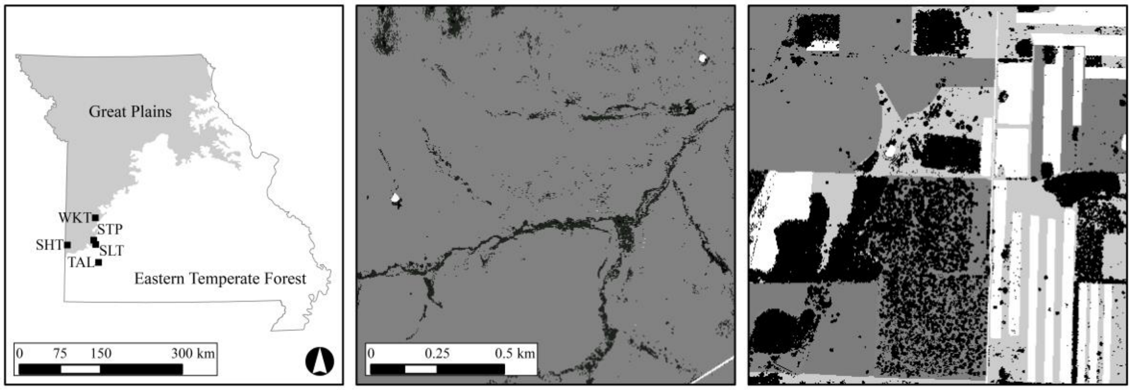

Figure 2.1. Location of 5 study sites in southwest Missouri: Shawnee Trail (SHT), Shelton (SLT), Stony Point (STP), and Talbot (TAL) Conservation Areas and Wah'Kon-Tah Prairie (WKT). Center panel illustrates a portion of an extensively managed site consisting of native grassland (dark gray) and woody cover (black). Right panel illustrates a portion of an intensively managed site that includes food plots (white) and (light gray).

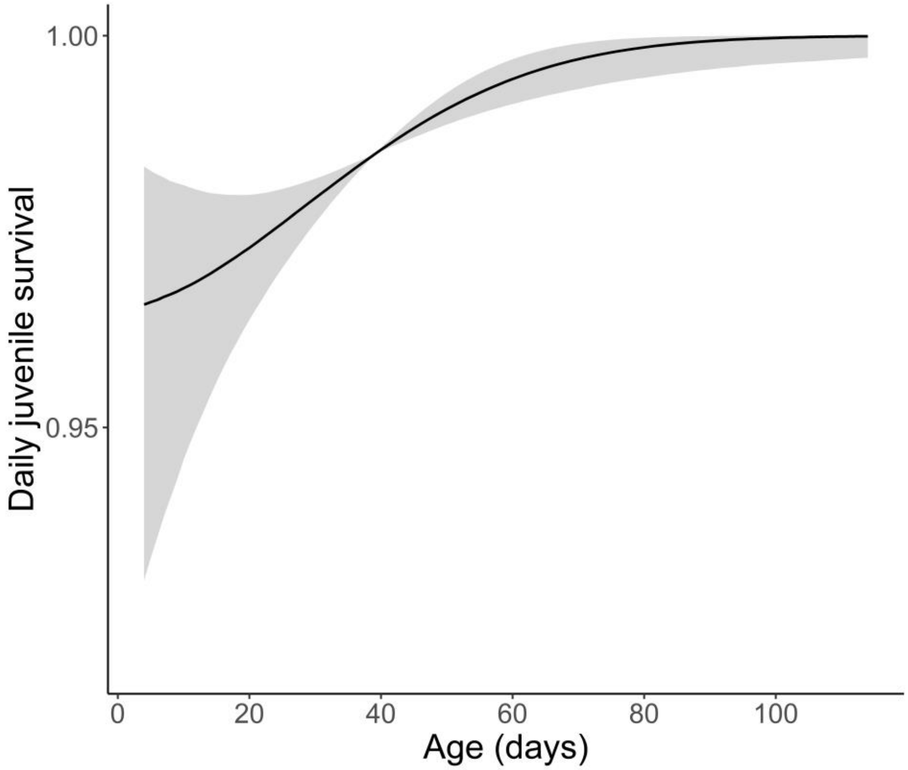

Figure 2.2. Mean (line) and 95% CRI (ribbon) predicted daily survival of northern bobwhite from hatch to 114-days old in southwest Missouri 2016–2018.

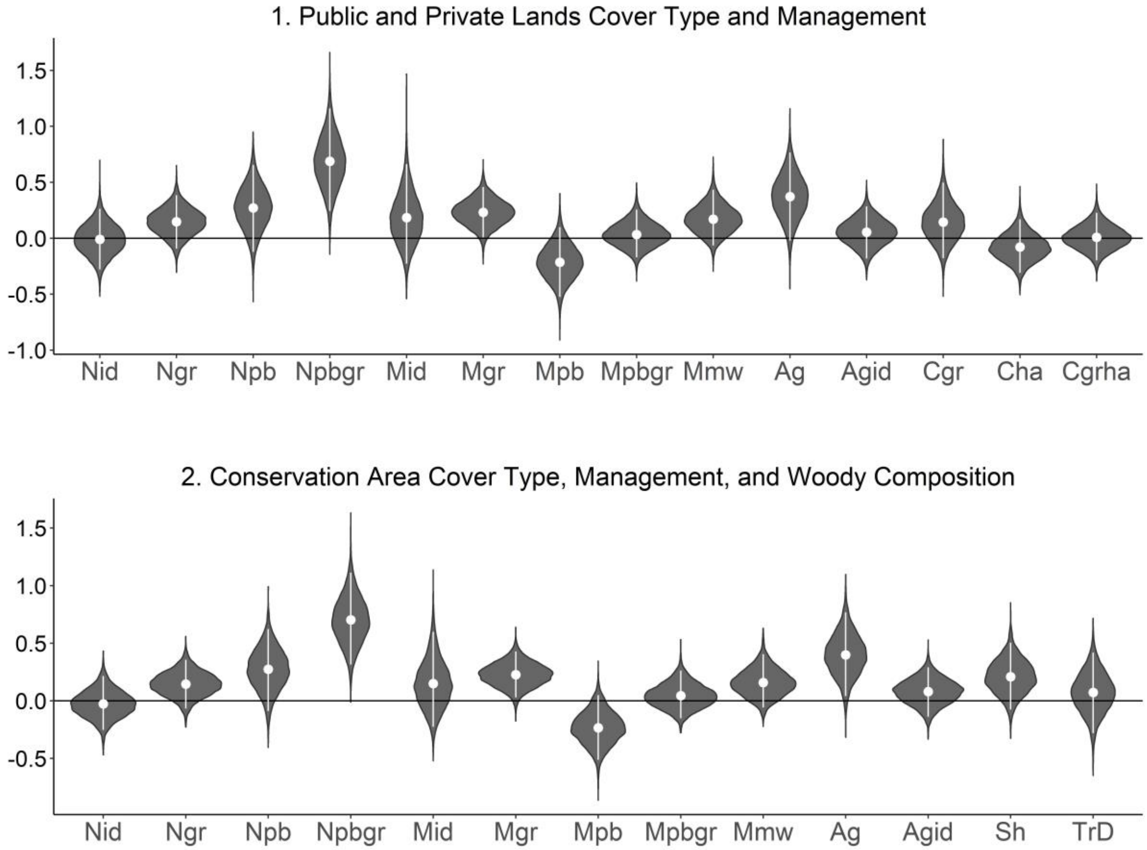

Figure 2.3. Mean (point) and 95% CRI (bar) and posterior distribution (shaded area) of effect sizes of local cover type and management on northern bobwhite juvenile survival in southwest Missouri 2016–2018 from our two most supported models. See Table 1 for abbreviations.

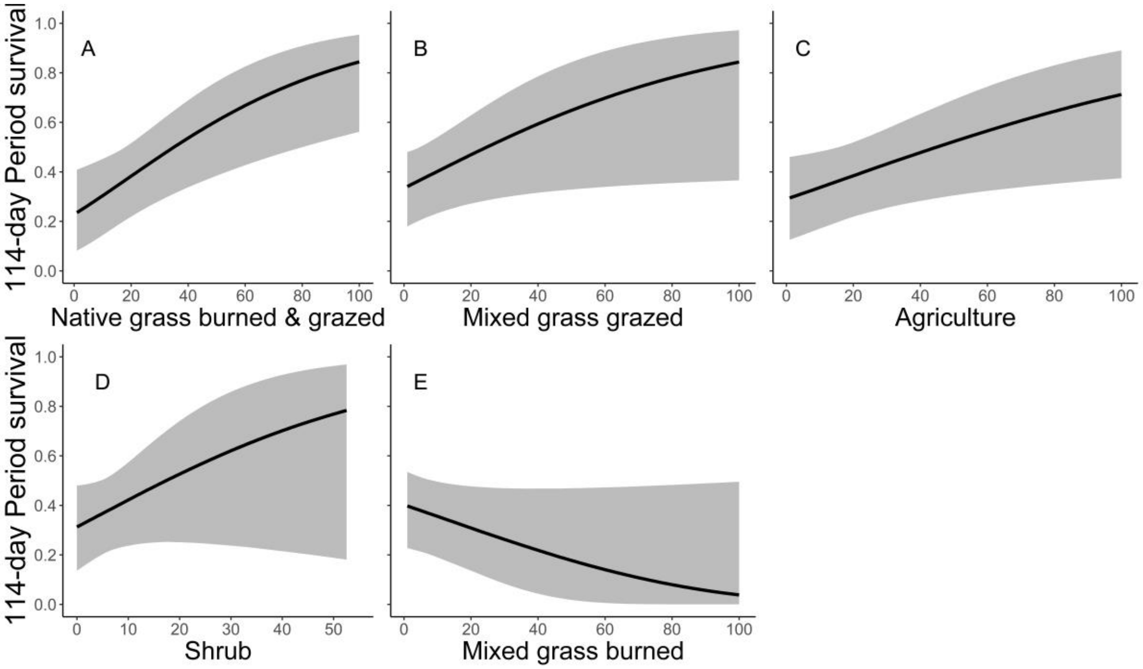

Figure 2.4. Mean (line) and 95% CRI (ribbon) predicted 114-day period survival of juvenile northern bobwhite based on credible effects from top-ranking cover type and management models describing percent cover within 50 m of daily locations in southwest Missouri 2016–2018.

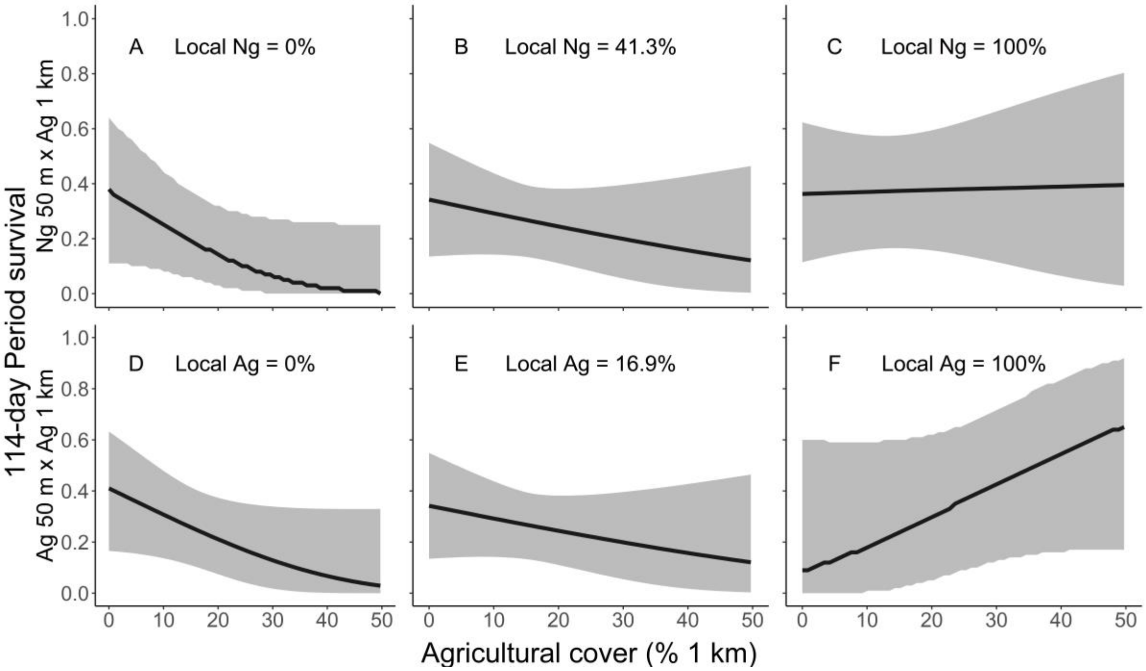

Figure 2.5. Mean (line) and 95% CRI (ribbon) predicted 114-day period survival of juvenile northern bobwhite demonstrating interactive effects of landscape-level agricultural composition (% within 1 km) and local native grassland (Ng) and agricultural (Ag) cover (% within 50 m) in southwest Missouri 2016–2018.

CHAPTER 3

BOBWHITE BROOD HABITAT SELECTION AND MOVEMENT DECISIONS ARE INFLUENCED BY AGE AND EXPLAIN EARLY LIFE SURVIVAL

ABSTRACT

Resource selection is a dynamic behavioral process driven by habitat valuation and risk avoidance on heterogeneous landscapes. Habitat selection and movement decisions of individuals may be sensitive to intrinsic factors, such as body condition, and variation in these choices may have consequences on subsequent survival. We evaluated population-level, age-specific patterns in northern bobwhite (*Colinus virginianus*) brood resource selection behavior to examine changes in habitat utility and availability within the juvenile development period using integrated step selection analysis within a Bayesian hierarchical modeling framework. Broods showed strongest selection for native grasslands that were both burned and grazed at least once in the previous two years and agricultural fields. We detected age-specific differences in selection and movement. Brood mobility improved with age; broods >35-days old travelled farther on average and took daily steps >200-m more frequently than younger age classes. Young broods 1- to 14-days old avoided idle native grasslands, while broods over 35-days old selected for that habitat. Young broods also selected areas farther from trees compared to older broods. We evaluated the survival consequences of resource selection behavior by comparing patterns in choices of broods that succeeded to choices of broods that failed to survive to 35-days old. Successful and failed broods younger than 35-days old differed in their selection for woody vegetation. Successful broods selected areas with greater percent shrub cover and areas farther from trees compared to failed broods. For young

animals, habitat utility may change during the course of development and early habitat choices can have fitness consequences.

INTRODUCTION

Movement and habitat selection behaviors of individuals determine population-level distributions across heterogeneous landscapes (Lima and Zollner 1996, Hobbs 2003). Individuals make non-random choices that are perceived to maximize net quality of available food, cover, and other resources contributing to survival and reproductive success (i.e., fitness; Cooper and Millspaugh 1999). Patterns in the choices of individuals and populations reflect resource requirements and the relative value of environments available to an individual or population (Johnson 1980). Resource selection behavior is a spatial process describing animal movements through a variable landscape (Thurfjell et al. 2014, Avgar et al. 2016). Individuals tend to stay within or move towards environments perceived to maximize resource quality and minimize predation risk (Lima and Zollner 1996, Nielsen et al. 2010, Dinkins et al. 2012, De Cesare et al. 2014, Atuo and O’Connell 2018).

Resource selection behavior is spatially and temporally hierarchical; population distributions and individual home ranges incorporate seasonal and diel patterns of movement and resource valuation among animal populations (Johnson 1980, Schooley 1994, Mayor et al. 2009, Dzialak et al. 2012). Selection behavior also varies by individual and can be influenced by intrinsic factors such as life stage, breeding status, age, and body condition (Paasivaara and Pöysä 2008, Ayers et al. 2013, Brooke et al. 2015, Jenkins et al. 2017a, Jenkins et al. 2017b, Kane et al. 2017). For young animals, habitat choices and movement patterns may be influenced by age and development (Anders et al. 1998, Rush and Stutchbury 2008, Goddard et al. 2009, Shipley et al. 2013, Wiltermuth et al. 2015, Jenkins et al. 2017b).

Northern bobwhite (*Colinus virginianus*; hereafter bobwhite) are an early successional, disturbance-dependent species experiencing range-wide declines on rapidly-changing landscapes (Brennan 1991, Williams et al. 2004, Hernandez et al. 2013). Productivity and recruitment contribute significantly to bobwhite population stability and growth (Williams et al. 2012, McConnell et al. 2018). Nest-site characteristics have been well studied for bobwhite; vegetation must provide adequate cover to conceal incubating adults and nests from predators and protect them from heavy rainfall or temperature extremes (Klimstra and Roseberry 1975, Burger et al. 1995a, Potter et al. 2011, Collins et al. 2009, Lusk et al. 2006, Townsend et al. 2001, Carroll et al. 2015). Although less is known about patterns of habitat selection during the brood phase, habitat must facilitate movement and foraging activities of young.

Many factors such as dispersal from nesting habitat, nutritional requirements, predation pressure, weather, and mobility can explain brood habitat selection and movement decisions (Sonerud 1985, Rotella and Ratti 1992, Tanner et al. 2017). Precocial young may travel large distances from nesting to brood-rearing habitat the first week after hatch (Sonerud 1985, Rotella and Ratti 1992, Mainguy et al. 2006, Goddard and Dawson 2009). The relative utility of available habitats may evolve during the brood stage as young flightless chicks grow more independent and mobile. Patterns of habitat selection and movement also likely cascade to influence survival of young (Rotella and Ratti 1992, King et al. 2006, Mainguy et al. 2006, Goddard and Dawson 2009).

On conservation areas in the eastern tallgrass prairie region of Missouri a variety of management techniques are used to maintain an early successional landscape and improve wildlife habitat; however, information on the relative quality of these management techniques for providing suitable bobwhite brood habitat is lacking. Prescribed burning with and without cattle grazing are used on prairies managed by the Missouri Department of Conservation (MDC) to replicate historical disturbances historically occurring on native prairies. Mechanical and chemical methods are used to control encroaching woody vegetation and invasive species are also employed. These disturbance regimes likely influence habitat utility for bobwhite broods (Sandercock et al. 2014, Brooke et al. 2017). Grasslands managed with fire, grazing, or both may have greater utility than idle grasslands for bobwhite broods, as these disturbances open up bare ground and increase plant diversity and arthropod abundance (Taylor et al. 1999, Engle et al. 2008). Woody vegetation structure and composition within these grassland habitats may also influence brood choices. Broods may select for local habitats with greater shrub cover, which provide shelter from predators and thermal protection (Carroll et al. 2015, Unger et al. 2015, Brooke et al. 2017). Trees, on the other hand, may be avoided by broods as they provide perches for aerial predators and habitat for mesocarnivores such as Red-tailed hawks, *Buteo jamaicensis*, and raccoons, *Procyon lotor* (Dzialak et al. 2012). Agricultural croplands are available to broods within and surrounding conservation areas. Intensively managed conservation areas maintain small units of agricultural crops and food plots for wildlife use. Much of the private lands surrounding conservation areas in southwest Missouri has been converted to introduced cool-season grasses (tall fescue, *Festuca arundinacea*), allowed to grow up into closed canopy woodland, or converted into fields of corn, soybeans, and wheat. Broods may avoid introduced cool-season pasture and agricultural crops as monocultures provide marginal foraging habitat and expose young to precipitation and temperature extremes (Palmer et al. 2001, Stanton et al. 2018). The extent to which broods select habitats in a heterogeneous landscape of agriculture and grassland reflects the relative value of different vegetation communities and management strategies to growth and survival.

We evaluated daily bobwhite brood movements and habitat selection patterns in southwest Missouri using integrated step selection analysis (iSSA), a recently-developed Resource Selection Function (RSF; Avgar et al. 2016). RSFs are a broad class of models which evaluate individual- and population-level selection patterns by comparing used and available habitats in a case-control sampling design (Manly et al. 1993). Conditional logistic regression (CLR) is an RSF modeling framework that allows matched comparisons of used and available habitats (Cooper and Millspaugh 1999). Under this approach, habitat availability is defined by an individual's location and mobility, which shifts as an individual moves across a landscape over time. iSSA extends the CLR framework to characterize both movement and habitat selection processes by incorporating step length and turning angle distributions into the evaluation of resource selection behavior (Fortin et al. 2005, Forester et al. 2009, Thurfjell et al. 2014, Avgar et al. 2016).

We evaluated population-level movement and habitat selection behaviors of bobwhite broods across a heterogeneous landscape of extensively managed native grasslands, intensively or traditionally managed conservation areas, and surrounding private lands. Extensively managed sites were large continuous tracts (320–3030 acres) of remnant or reconstructed prairies managed primarily by prescribed burning, conservation grazing, and mowing practices. Intensively managed sites applied traditional, fine-scale practices incorporating agricultural food plots, grass strips, and woody edge cover among grassland units managed with prescribed burning and some conservation grazing. The contribution of variation in individual behavior to population-level processes has not been thoroughly addressed in applied ecological research (Merrick and Koprowski 2017). We considered how resource selection behaviors varied with brood age and fate, and accounted for brood-level variation in a hierarchical iSSA framework. Our objectives were to (1) evaluate stage-specific habitat selection and movement patterns of young, flightless broods ≤14-days old, dependent broods 15- to 35-days old, and independent broods >35-days old, and (2) compare early period resource selection patterns of young broods that survived to 35 days to those broods that failed. We hypothesized brood habitat selection and movement patterns would vary with age as mobility, foraging, and predator evasion behaviors change with development of precocial young such as bobwhite. We also hypothesized selection behavior of young broods would explain variation in survival whereby choices of broods that succeeded would differ from those that failed.

METHODS

Study Area

We characterized herbaceous cover, woody vegetation structure, and management practices across our study extent and quantified daily step length distributions of radio-tagged birds. We followed tagged individuals on five MDC conservation areas and neighboring private lands from June 1 to as late as December 13 2016–2018 (Fig. 3.1). Shawnee Trail (3635 acres) and Robert E. Talbot Memorial Conservation Areas (4361 acres) were intensively managed sites. These areas incorporated narrow rows of strip crops and woody field borders among larger grassland units, providing food and cover for wildlife in smaller management units (4–60 acres; Fig. 3.1). Management included prescribed burning, conservation grazing, disking, and woody and invasive species encroachment (herbicide and mowing). Wah'Kon-Tah Prairie (3030 acres), Stony Point Prairie Conservation Area (960 acres), and Wade and June Shelton Memorial Conservation Area (320 acres) were extensive native grasslands managed with fire, grazing, and mowing (Fig. 3.1). Private lands surrounding these conservation areas were primarily cool-season grazing pastures and hayfields (*Festuca arundinacea*, *Dactylis glomerata*, *Phleum pratense*), closed canopy woodland, with agricultural fields of corn (*Zea mays*), soybean (*Glycine max*), and winter wheat (*Triticum* spp.) in some areas.

Brood tracking and captures

We monitored bobwhite brood resource selection and movement patterns daily using radio-telemetry. Most bobwhite broods were tracked from hatch. Some broods were opportunistically tracked post hatch as radio-tagged adults who did not participate in nest incubation were discovered attending broods. For broods ≤3 weeks old, habitat choices were determined by tracking radio-tagged attending adults. For broods >3 weeks old, we used locations of radio-tagged juveniles to evaluate brood resource selection patterns if attending adults were depredated or abandoned their independent young. We found young brood-mates tended to move together as a unit through the summer and into fall even without an attending adult present.

We captured broods over two weeks of age using the corral technique and a thermal imaging camera before first light (Smith et al. 2003, Andes et al. 2012). Our corrals were built 1 m tall with a PVC pipe frame and panel walls made from extra-strength window screen. We also used garden netting as a tent over the corral to prevent individuals from flushing out on capture. We sutured radio-tags on one to six juveniles per brood weighing over 20-g with 0.6 to 0.8-g transmitters (American Wildlife Enterprises, Monticello, FL, USA), which had 45 to 60-days of expected battery life (Carver et al. 1999, Burkpile et al. 2002, Dreitz et al. 2011, Terhune et al. 2020). Transmitters never exceeded 4% of a juvenile's body mass. We attached transmitters low on the back, below the scapula along the thoracic vertebrae, and clipped antennae 7-cm to avoid entanglement in grasses (Terhune et al. 2020).

Broods were tracked on average 6 days per week and observations with at least two consecutive daily locations were included in our resource selection analysis as a used step. We rotated the order of individuals tracked and collected at least one roost location before first light each week. Broods were tracked to within 10 m of their location each day unless they were in inaccessible, such as on restricted private lands, in which locations were triangulated. All brood locations were projected from the observers' UTM, distance, and azimuth data. We collected data on cover type, management, and woody vegetation composition using maps derived from field observations, remotely sensed land cover data, and LIDAR data for each brood location. All animal procedures were approved under University of Missouri Animal Care and Use Committee protocol #8766.

Habitat Covariates

We included habitat covariates representative of the structural and compositional diversity of conservation areas and their surrounding private lands. Classification of herbaceous cover types, management practices, and woody vegetation structure were informed by bobwhite ecological literature and applied management objectives. Herbaceous cover types included agricultural row crop (Ag), idle agricultural fields (Agid), native grass (N), mixed grass (M), and cool-season grass (C) and were characterized by percent cover within a 50 m radius for each used and available location (Table 1). We further characterized grassland cover types by management practices using a 2-year-burning (pb) and grazing (gr) history, a within-year mowing history (mw), or we classified grasslands as idle (id) if no management had occurred over a two-year period (Table 3.1). For example, the category Npbgr indicates native grassland habitat that has been burned and grazed within a two-year management history, while Ngr indicates native grassland habitat that was only grazed at least once in the previous two years. These cover types were largely classified from field observations and maps from wildlife managers, but some private lands outside conservation areas were classified using 2018 CropScape and 2016 NAIP datasets (USDA 2016, USDA 2018).

We characterized woody vegetation composition and configuration as either percent shrub (Sh) or tree cover (Tr) within 50 m and distance to nearest tree (TrD; m) from each used and available location. Shrub and tree cover were mapped using LIDAR data. We created a digital surface model (DSM) and a digital elevation model (DEM) at 3.6 m resolution and calculated their difference to estimate vegetation height in ArcGIS. We classified elevations of 0 to 0.7 m as ground cover, 0.7 to 3.5 m as shrub cover, and 3.5 to 40 m as tree cover. We validated woody cover classification by comparing results with ground-truthed GPS points and NAIP aerial imagery across the study extent.

Used-available sampling design

We simultaneously evaluated effects of bobwhite brood age on habitat selection and daily movement decisions in a conditional logistic regression that included both a habitat utilization kernel and a movement kernel (Avgar et al. 2016). We incorporated spatial processes into a biologically meaningful sample of availability by drawing control points from an empirical distribution of observed movements (Fortin et al. 2005, Rhodes et al. 2005, Forester et al. 2009, Thurfjell et al. 2014). To sample random step lengths, we used mean $\overline{L}$ and variance σ_L^2 of calculated Euclidean distance (m) between observed consecutive daily locations to estimate shape σ_0 and scale μ_0 parameters describing a log-normal distribution of daily distance travelled (Eq. 1, Eq. 2; Fortin et al. 2005). We sampled random step headings from a uniform distribution between 0 and 2Π. We sampled 10 available locations for every 1 used location by projecting 10 randomly sampled step lengths and turning angles from the start point of each observed step. Habitat characteristics at end points of each used step were then compared to projected end points of each available step. Step lengths observed were also compared to step lengths drawn from an empirical distribution of brood movements.

$$\sigma_0 = \sqrt{\ln\left(1 + \frac{\sigma_L^2}{\overline{L}^2}\right)} \quad (1)$$

$$\mu_0 = \ln\left(\frac{\overline{L}}{\sqrt{1+\frac{\sigma_L^2}{\overline{L}^2}}}\right) \qquad (2)$$

Hierarchical Bayesian selection model

We estimated the probability (*P*) brood (*n*) in age or fate class (*k*) would use location (*j*) with habitat features (*m*) at time (*t*) given a set (*J*) of available steps and locations(*i*) where $i \neq j$ using a conditional logistic regression ($P(x_{njktm})$; Eq. 3). Habitat selection behavior was attributed to multiple cover type and management predictors *m* observed at the end point of each daily used step *H*(x_{njtm}) and each daily available step *H*(x'_{nitm}). Habitat selection behavior was quantified in as a vector of habitat coefficients describing selection for each brood and each age or fate class (β_{nkm}; Eq. 3). Movement patterns were estimated from observations of daily distance travelled (L_{njt}) and quantified in the movement coefficient vector α_{nk} for each age and fate class. Variation in selection and movement among age classes and between broods that survived and broods that failed at 35 days were evaluated via an interaction with a class dummy variable, S_{nkt} (Eq. 3; Cooper and Millspaugh 1999, Bloom et al. 2013). The linear function representing the utility (U) of location j at time t to brood n for class k, (U_{njtkm}), provided by a set of *m* habitat resources is $U_{njktm} = \beta_{nkm} \cdot x_{njtm} \cdot S_{nkt}$

$$P\left(x_{njktm}\right) \frac{\exp[\, \beta_{nkm} \cdot H\left(x_{njtm}\right) \cdot S_{nkt} + \alpha_{nk} \cdot \ln(L_{njt})^2 \cdot S_{nkt}]}{\sum_{i=0}^{J} \exp[\beta_{nkm} \cdot H(x'_{nitm}) \cdot S_{nkt} + \alpha_{nk} \cdot \ln(L'_{nit})^2 \cdot S_{nkt}\,]} \qquad (3)$$

We implemented our iSSA in a hierarchical Bayesian framework to account for individual- and population-level variation through random sampling (Gilles et al. 2006). Utilities were estimated as a random variable specific to an individual's location at each time step in a mixed multinomial logit model (Duchesne et al. 2010). This model structure included prior distributions for brood-level parameters (Eq. 5), and hyperparameter distributions for population-level selection parameters (Eq. 6; Thomas et al. 2006). Brood-level random regression coefficient vectors for habitat selection, β_{nkm} and movement, α_{nk}, represented samples of population-level resource selection behavior (Gilles et al. 2006, Thomas et al. 2006). Hyperparameter vectors, β_{km}^* and α_k^*, described mean population-level selection behavior and their precision, $\sigma_{\beta km}^*$ and $\sigma_{\alpha k}^*$ (Thomas et al. 2006).

$$\beta_{nkm} \sim dnorm(\beta.H_{km}^*, \sigma.H_{km}^*) \qquad (5)$$

$$\alpha_{nk} \sim dnorm(\alpha.M_k^*, \sigma.M_k^*)$$

$$\beta.H_{km}^* \sim dnorm(0, 0.0001) \qquad (6)$$

$$\alpha.M_k^* \sim dnorm(0, 0.0001)$$

$$\sigma.H_{km}^* \sim dgamma(0.01, 0.01)$$

$$\sigma.M_{\alpha k}^* \sim dgamma(0.01, 0.01)$$

Candidate model development and evaluation

We evaluated a set of cover type and management parameters representative of habitat available on public and private lands. This set included agricultural row crop (Ag; corn, soybean, sunflower *Helianthus annuus*, winter wheat), idle agriculture (Agid), native grasslands that were idle (Nid), grazed (Ngr), burned (Npb), or mowed/hayed (Nmw), and mixed grasslands that were idle (Mid), grazed (Mgr), burned (Mpb), or mowed (Mmw). We examined collinearity among habitat covariates within models and avoided combinations of covariates that resulted in a variable inflation factor (VIF) >2.5 and excluded cool-season grasslands to avoid multicollinearity. Because of the relative nature of parameter effects in conditional logistic regression, we used the same set of parameters to evaluate resource selection behavior by age at the population level and to evaluate effects of choice on young brood survival to 35-days old.

To address objective 1, stage-specific resource selection effects were considered for agriculture, idle native grasslands, shrub (Sh) and tree cover (Tr), distance to trees (TrD), and daily step length distributions (Step; Table 3.1). This set of available cover types were evaluated for age-specific effects as the most parsimonious set of variables that estimate (1) the value of agricultural units available to broods on intensively managed sites and surrounding private lands, (2) the importance of disturbance on native grassland utility, (3) the influence of woody composition on habitat choice, and (4) changes in habitat availability with growth and development. Brood age classes were classified based on the ages at which young can fly short distances (14 days) and females may abandon a brood to attempt a second nest (35 days). A three-stage model included broods that were flightless ≤14-days old, dependent 14- to 35-days old, and independent >35-days old. A two-stage model compared young broods ≤35-days old and old broods

>35-days old. A single-stage model included no age class information. To address objective 2, we subset our data to include observations of young broods ≤35-days old whose fate at 35 days was known. We compared selection for agriculture, idle native grasslands, shrub and tree cover, distance to tree, and daily step length distribution of successful and failed dependent broods ≤35-days old to estimate the influence of choice on survival of young.

We inspected trace plots for mixing across Markov chains, checked that Rhat test statistics were <1.1, and that posterior effective sample sizes were >200 for all model parameters to ensure models converged (Brooks and Gelman 1988, Gelman and Hill 2007, Link and Barker 2010, Kéry and Schaub2012). We evaluated model performance by ranking models based on WAIC and interpreting the top model (Watanabe 2010).

RESULTS

Population-level Brood Habitat Selection and Movement

We monitored resource selection behavior of 101 bobwhite broods for a total of 2,788 step choice-sets 2016–2018. These data contained 627 steps from 80 broods ≤14-days old, 1092 steps from 91 broods 15- to 35-days old, and 1071 steps from 45 broods 36 to 114-days old. Ranges of habitat and step length data for used and available locations are summarized in Table 1. We included all brood observations from our data for our population-level, age-specific, step- selection analysis; including successful broods, failed broods, and broods eventually lost due to dropped collars, loss of transmitter signal, or movement onto restricted private lands. The proportion of posterior parameter distributions greater than or less than zero indicate the strength of selection for or against each habitat, respectively.

All habitat selection models performed better than the null model (Table 3.2). Models containing stage-specific estimates for habitat selection and step length distribution performed better than the model that did not consider effects of age class (ΔWAIC = 105.2; Table 3.2). We focused interpretation on the top-ranked model because it had substantially more support than the other models. It included parameters for habitat selection and step length distribution for three stages: flightless broods ≤14-days old, dependent broods 15- to 35-days old, and independent broods over 35-days old.

Broods showed the strongest selection among native grasslands for areas that were burned and grazed within the past two years, followed by areas burned only, and mowed (Fig. 3.2, Fig. 3.3, Table 3.3). Broods showed no selection for native grasslands that were grazed only (Fig. 3.2, Table 3.3). Older broods (S[2]) selected for idle native grasslands, whereas the youngest age class (S[0]) weakly avoided idle native grasslands ($f = 0.74$; Fig. 3.2, Fig. 3.5, Table 3.3). Among mixed grasslands, bobwhite selected for areas mowed in that year. All age classes selected for agricultural row crop and idle agricultural fields (Fig. 3.2, Fig. 3.4, Table 3.3). Among woody habitat components, broods selected for shrub cover, weakly avoided tree cover, and avoided locations further from trees (Fig. 3.2, Fig. 3.4, Table 3.3). Selection for shrub cover and avoidance of areas farther from trees was stronger for older broods than younger broods (Fig. 3.4). Broods ≤14-days old took shorter steps on average and travelled <200 m in a day more frequently than older age classes, while broods >35-days old took longer steps on average and travelled >200 m more frequently than younger age classes (Fig. 3.5, Table 3.3). The

95th percentile of our step length distribution curves for young flightless broods ≤14-days old, dependent broods 15- to 35-days old, and independent broods >35 days were 309 m, 334 m, and 404 m respectively.

Habitat Selection and Movement of Successful and Failed Young Broods

We evaluated habitat choice and movement of 80 broods ≤35-days old to compare resource selection behavior between broods that did and did not survive to 35-days old. These data contained 273 steps from 29 failed broods, F[0], and 1187 steps from 51 successful broods, F[1]. We removed 21 broods from this analysis because brood fate was unknown due to attending adult mortality, dropped radio-tags, or because we were unable to track broods on restricted private lands.

Our top model suggested brood resource selection differed between broods that failed and broods that succeeded in surviving to 35 days because it performed better than our null model without fate classes (ΔWAIC = 2.3; Table. 3.2). We did not detect a difference in selection for agricultural cover, tree cover, or daily step lengths between broods that failed and broods that survived to 35 days, however there were differences in selection for shrub cover and distance to trees (Fig. 3.6, Table 3.3). Broods that failed weakly avoided shrub cover, while broods that succeeded selected for shrub cover and were more likely to use local habitat with greater percent cover (Fig. 3.7, Table 3.3). Both failed and successful broods avoided areas further from trees than randomly available (Fig. 3.6, Table 3.3). However, broods that failed were more likely to select areas closer to trees than broods that succeeded, and broods that succeeded were more likely to select areas farther from trees than broods that failed (Fig. 3.6, Fig. 3.7, Table 3.3). For idle native grassland cover, mean estimates were similar and posterior samples showed 83.4% support of a positive selection for failed broods and 75.8% support of a positive selection for successful broods (f-values: proportions of samples that do not span zero; Fig. 3.6, Table 3.3).

DISCUSSION

Bobwhite broods showed the strongest selection for native grasslands that were both burned and grazed at least once within the previous two years. We also found habitat selection patterns changed with age. Young broods avoided idle native grasslands, while older broods selected for those habitats. Selection for shrubs increased with age and older broods selected areas closer to trees compared to young broods. We found variation in these choices had consequences on early life survival. Selection for woody cover differed between young broods that survived to 35 days and young broods that failed. Broods that survived were more likely to choose areas with greater percent shrub cover and areas farther from trees than broods that failed. We evaluated movement as a behavioral component of resource selection and found daily distance travelled increased with age, but movement patterns did not differ between broods that succeeded and broods that failed to 35 days.

Quantifying population patterns from a sample of individual choices

Resource selection behavior is evaluated from observations of daily choices among individuals. To make inference on population-level patterns, we accounted for bias associated with unbalanced, correlated observations of individual animals, dependence of local availability on choice, and animal movement patterns within a Bayesian hierarchical modeling framework (Gilles et al. 2006, Thomas et al. 2006, Duchesne et al. 2010). Brood-level random regression coefficients in the conditional logistic likelihood function address problems of non-independence among consecutive observations of individuals, differences in availability and preferences among individuals, and unbalanced data across individuals sampled (Follmann and Lambert 1989, Mysterud and Ims 1998, Otis and White 1999, Leban et al. 2001, Gilles et al. 2006, Duchesne et al. 2010, Pearish et al. 2013). We incorporated brood-level random regression coefficients and interpreted hyperparameters of our top models for population-level inference.

Methods evaluating selection patterns can also address bias in selection estimates associated with interactions between individuals and characteristics of their local environment by incorporating animal movement information into sampling and modeling approaches (Fortin et al. 2005, Forester et al. 2009, Avgar et al. 2016). Sampling available, but unused habitats from an empirical distribution of observed movements and incorporating a resource-independent movement kernel into a conditional logistic regression model reduces bias in selection estimates (Forester et al. 2009). We evaluated daily choices of bobwhite broods by comparing endpoints of used steps to endpoints of 10 available steps sampled from a log-normal step length distribution of observed daily bobwhite brood movements.

Population-level habitat selection

Broods likely selected for burned and grazed native grassland habitats because those diverse, disturbed prairie plant communities provided open bare ground and high invertebrate abundance for improved mobility, foraging, growth, and survival (Hurst 1972, De Vos and Mueller 1993, Taylor et al. 1999, Collins et al. 2009, Doxon and Carroll 2010, Kentie et al. 2013, Brooke et al. 2017, Chapter 2). Coupling grazing and fire on tallgrass prairies promotes heterogeneity in vegetation structure and composition (Fuhlendorf and Engle 2004). Grazing enhances light and nitrogen availability on the ground, reduces dominance of grasses, and increases plant species richness and diversity (Veen et al. 2008). Patch burning on grazed prairies can also produce invertebrate prey for bobwhite broods who require high protein diets for rapid growth (Nestler et al. 1942, Engle et al. 2008). These interactive disturbances can facilitate brood movement and foraging activities, but also leave adequate overhead cover. There are clear fitness benefits to this resource selection behavior: bobwhite juvenile survival is higher on native grasslands that are both burned and grazed at least once in the last two years compared to other native and non-native grassland habitats (Chapter 2).

We also found broods selected for native grasslands that were burned, but not grazed in the previous two years. Small, patchy prescribed fires remove accumulated litter to create open foraging habitat in close proximity to thicker roosting habitat (Taylor et al. 1999, Kamps et al. 2017). This can reduce brood home range size, which is indicative of improved habitat quality (De Vos and Mueller 1993). By comparison, we found broods did not select for native grasslands that were grazed, but not burned in the previous two years. Light to moderate grazing that leaves adequate vegetation height for cover can benefit broods, but fire is an important component of that of that disturbance regime (Sutter and Ritchison 2005, Harper et al. 2015, Chapter 2).

Contrary to our predictions, we found broods selected for both native and mixed grasslands that were mowed or hayed within a breeding season. We expected broods would avoid cut grasses because these practices remove cover, cause litter accumulation, and may not improve plant diversity or habitat structure for bobwhite broods (McCoy et al. 2001, Taylor et al. 1999, Gruchy and Harper 2014). Mowing/haying may negatively influence survival through direct mortality of broods or indirectly through increased rates of depredation of young in vegetation that reduces cover (Bollinger et al. 1990). Timing of the management practice may explain differences between predicted and observed effects in our study. Mowing and haying of native grasses typically happened in late summer after peak nesting season, meaning units were not cut for much of the brood season (Harper et al. 2007, Birckhead et al. 2014). Mowing also only changes vegetation structure temporarily. Grass canopy can grow to heights that provide adequate cover for broods within a few weeks of harvest (Birckhead et al. 2014). While we did not have weekly data available on mowing practices across our study extent, a finer-scale, within-season evaluation may better capture the effects of mowing/haying practices on brood resource selection patterns.

Age-dependent mobility and habitat selection

Non-environmental factors can influence habitat selection behaviors (Jones 2001). For precocial young that leave the nest soon after hatching, age strongly influences development and mobility. Individual physical condition can affect resource selection behavior by influencing perceived habitat quality and how an individual moves across a landscape (Merrick and Koprowski 2017). The first 35 days of life are a critical period for success of bobwhite broods and during this time broods may exhibit resource requirements and selection behavior unique to later stages of development (Lusk et al. 2005, Hannon and Martin 2006). We found that bobwhite broods exhibited age-specific differences in movement and habitat selection.

Age influenced daily distances travelled by broods and the habitat available to them. The radius of habitat available to broods older than 35-days increased by just over 30% within a 114-day development period. A study conducted in mesquite-mixed brush habitat of southern Texas found daily home range size and minimum daily distances traveled nearly doubled from pre-fledging to post-fledging brood periods (0.7 ha and 277 m to 1.4 ha and 589 m respectively; Taylor and Guthery 1994). Post-fledging broods may travel more sinuously and may be better able to explore within their daily home ranges than pre-fledging broods.

Age can also influence the relative quality of different habitats as resource needs and risk perception change with development. Small flightless young survive to stages where they can thermoregulate, flush from predators, modify foraging behavior and diet, and potentially better use new habitats. Age and mobility there by interact with habitat selection behavior to influence selective pressures such as predation and weather exposure (Merrick and Koprowski 2017).

All age classes of bobwhite broods in our study selected for row crop and idle agricultural habitat. We expected young broods to avoid row crops due to poor insect prey abundance or availability (Taylor and Burger 2000). Bobwhite use agricultural areas during brood-rearing periods, however, foraging rates and growth of bobwhite chicks are low within soybean, corn, and wheat fields compared to field borders and native grasslands, suggesting cropland provides suboptimal foraging habitat (Puckett et al. 1995, Palmer et al. 2001, Doxon and Carroll 2010, Lohr et al. 2011). Contrary to our hypothesis, we found all age-classes of broods selected for row crop and idle agricultural habitat. Agricultural land management and temporal variation in resource needs may account for selection behavior. Grassland vegetation strips within strip crop units or along field borders may provide adjacent foraging habitat in agricultural areas and pesticide restrictions on public lands allows annual weeds to grow in crop fields, which may provide habitat for sufficient insect prey populations (Doxon and Carroll 2007). We also did not account for temporal variation in resource selection patterns within a brood’s daily cycle. Behavioral shifts in selection within the diel cycle may be related to risk avoidance or maintaining suitable thermal environments (Dzialak et al. 2012). While foraging opportunities are limited in croplands, these habitats may be suitable for loafing or roosting periods; in agricultural fields broods could move easily along the ground, sight approaching ground predators, and crop canopy may provide adequate height and cover from aerial predators. While agricultural areas provide marginal foraging habitat, predator avoidance and improved juvenile survival may be a fitness benefit explaining selection patterns (Palmer et al. 2001, Chapter 2).

Bobwhite broods are less likely to occupy fields with dense grass and litter cover (Taylor et al.1999, Barnes et al. 1995, Osborne et al. 2012, Unger et al. 2015). We hypothesized thick grass and litter cover would be more limiting to small, flightless juveniles compared to larger, more mobile broods. We found young broods did avoid idle native grasslands, while older broods selected for those habitats. Size is an important factor mediating age-dependent habitat utility. Thick grasses reduce mobility, prey availability, and foraging rates of young bobwhite chicks 4- to 10-days old (<10 g), but not that of ring-necked pheasant young of the same age (>19 g; Doxon and Carroll 2010). With growth, older bobwhite broods were better able to move, forage, and utilize thick idle native grassland habitat.

Woody vegetation composition and structure are important components of brood habitat for this shrub-obligate species (Martin et al. 2009, Unger et al. 2015). We found older broods selected for shrub cover. Shrubs provide protection from warm daytime temperatures and escape cover from predators (Johnson and Guthery 1988, Carroll et al. 2015). We also found both younger broods and older broods selected areas closer to trees than randomly available, but, younger broods selected areas farther from trees compared to older broods. Young broods may avoid areas closer to trees than older broods because they cannot yet flush from predators; predator avoidance strategies may depend on age-specific behavioral responses to threats (Dinkins et al. 2012, De Cesare et al. 2014, Perkins et al. 2014). However, the overall pattern that the probability of selection decreased with distance from tree creates the potential for an ecological trap if predation is greater near trees and areas farther from predation risk are avoided (Patten and Kelly 2010).

Fitness consequences of resource selection behavior

While preferred habitats are often assumed to provide fitness benefits, ecological or perceptual traps may result in selection patterns of individuals or populations that do not optimize important demographic rates (Patten and Kelly 2010, Dzialak et al. 2011, De Cesare et al. 2014, Merrick and Koprowski 2017). Few studies link resource selection behaviors with demographic responses by examining survival consequences of variation in choices among individuals (Jones 2001, Aldridge and Boyce 2007, Bloom et al. 2013, De Cesare et al. 2014, Merrick and Koprowski 2017). Recent studies have found habitat composition, management, and suitability can influence survival of bobwhite young (Kamps et al. 2017, Tanner et al. 2019, Chapter 2). However, these studies have not addressed demographic consequences of individual-level variation in habitat selection behavior. We included survival information as an interaction with resource selection behavior parameters within our integrated step selection analysis to jointly evaluate fitness consequences of brood habitat and movement decisions (Cooper and Milspaugh 1999, Bloom et al. 2013).

Daily step lengths of bobwhite broods that failed were similar to movement choices made by broods that survived to 35 days. Impacts of movement on survival of precocial young are mixed. Larger movements early in the brood period and greater dispersal distances in fragmented landscapes may reduce brood survival (Rotella and Rati 1992, Hannon and Martin 2006). However, if quality nesting habitat is different than quality brood-rearing habitat, larger movements may result in better habitat for greater brood survival (Badyaev et al. 1996, Yerkes 2000, Paasivaara and Pöysä 2008). While distributions of daily step lengths were not significantly different among successful and failed broods in our study, more work is needed linking habitat-specific movement and dispersal patterns to bobwhite brood survival.

While average, population-level habitat selection patterns are assumed to be beneficial, variation in choices of individuals may affect brood fate. We found habitat selection for agricultural row crop, idle native grassland, and tree cover was similar for broods that succeeded and broods that failed to 35 days. However, habitat selection for woody cover, differed between successful and failed broods. As an important driver of breeding-season selection patterns, selection for woody cover accordingly influenced brood fate (Taylor and Burger 2000, Unger et al. 2015). Successful broods selected for areas with more shrub cover, while failed broods weakly avoided those areas. Attending adults choosing shrubby habitats with taller vegetation provide broods greater visual obstruction from aerial predators (Hannon and Martin 2006, Collins et al. 2009, Perkins et al. 2014). Taller vegetation can also create fine-scale thermal refuges during summer daytime peak temperatures; failure to choose more moderate microclimates under shrubby vegetation may lead to thermal stress for young (Scheffers et al. 2014, Carroll et al. 2015). While all young broods selected areas closer to trees than randomly available, successful broods selected areas farther from trees than failed broods, which supports previous work suggesting that bobwhite mortality risk is greater for those using forested habitat (Lohr et al. 2011).

CONCLUSION

Three questions related to patterns of habitat selection and movement decisions can help us more robustly understand animal distributions on modern landscapes: (1) Which habitats are animals choosing? (2) what influences that choice? (3) what are the fitness consequences of variation in choice? Variation in patterns of habitat selection and movement contains important information on how decisions relating resource valuation and risk aversion are affected by non-environmental factors and how those choices influence fitness outcomes. For bobwhite broods, age influenced resource selection behavior and choices affected brood survival to 35-days. Bobwhite preferred native grassland habitats, and areas disturbed by grazing and fire with available shrub cover were especially valuable for success of young broods.

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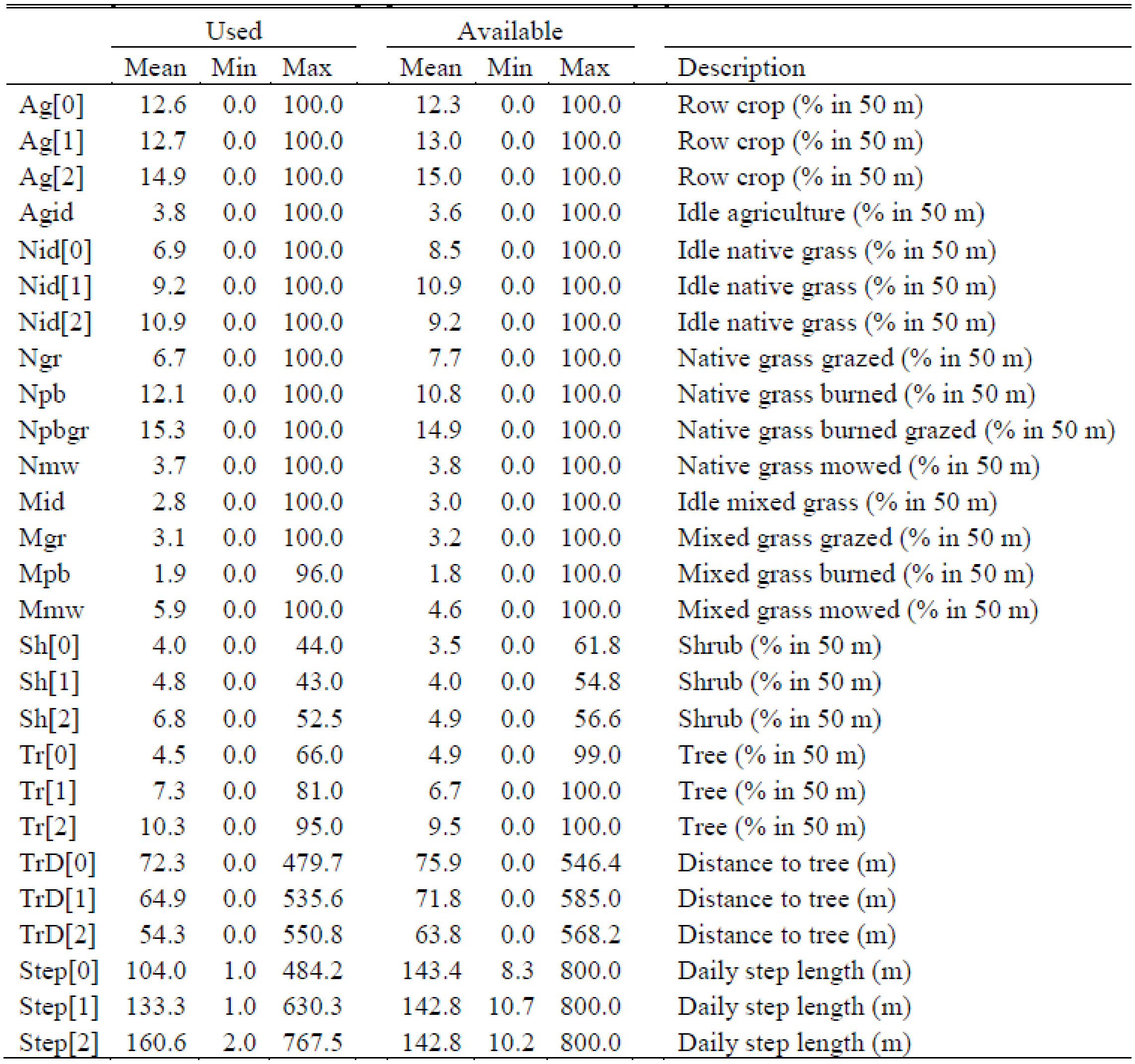
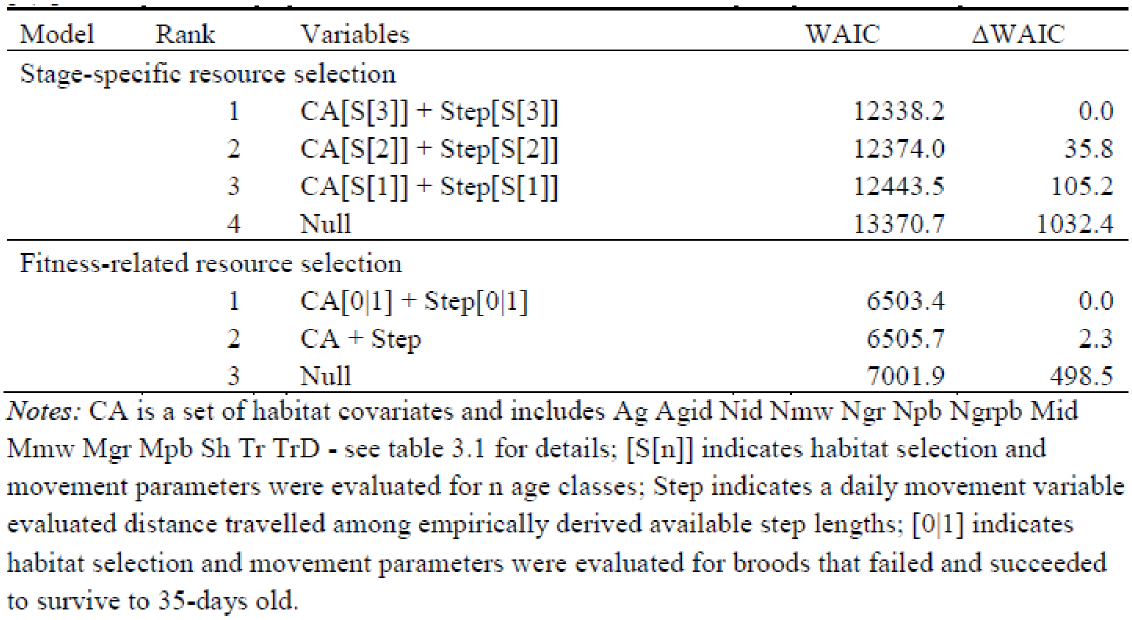
TABLES

Table 3.1. Description of habitat, woody vegetation composition and configuration, and step length variables for used and available locations across three stages of northern bobwhite broods ≤14-days old [0], 15- to 35-days old [1], and >35-days old [2] in southwest Missouri 2016–2018.



	Used			Available			
	Mean	Min	Max	Mean	Min	Max	Description
Ag[0]	12.6	0.0	100.0	12.3	0.0	100.0	Row crop (% in 50 m)
Ag[1]	12.7	0.0	100.0	13.0	0.0	100.0	Row crop (% in 50 m)
Ag[2]	14.9	0.0	100.0	15.0	0.0	100.0	Row crop (% in 50 m)
Agid	3.8	0.0	100.0	3.6	0.0	100.0	Idle agriculture (% in 50 m)
Nid[0]	6.9	0.0	100.0	8.5	0.0	100.0	Idle native grass (% in 50 m)
Nid[1]	9.2	0.0	100.0	10.9	0.0	100.0	Idle native grass (% in 50 m)
Nid[2]	10.9	0.0	100.0	9.2	0.0	100.0	Idle native grass (% in 50 m)
Ngr	6.7	0.0	100.0	7.7	0.0	100.0	Native grass grazed (% in 50 m)
Npb	12.1	0.0	100.0	10.8	0.0	100.0	Native grass burned (% in 50 m)
Npbgr	15.3	0.0	100.0	14.9	0.0	100.0	Native grass burned grazed (% in 50 m)
Nmw	3.7	0.0	100.0	3.8	0.0	100.0	Native grass mowed (% in 50 m)
Mid	2.8	0.0	100.0	3.0	0.0	100.0	Idle mixed grass (% in 50 m)
Mgr	3.1	0.0	100.0	3.2	0.0	100.0	Mixed grass grazed (% in 50 m)
Mpb	1.9	0.0	96.0	1.8	0.0	100.0	Mixed grass burned (% in 50 m)
Mmw	5.9	0.0	100.0	4.6	0.0	100.0	Mixed grass mowed (% in 50 m)
Sh[0]	4.0	0.0	44.0	3.5	0.0	61.8	Shrub (% in 50 m)
Sh[1]	4.8	0.0	43.0	4.0	0.0	54.8	Shrub (% in 50 m)
Sh[2]	6.8	0.0	52.5	4.9	0.0	56.6	Shrub (% in 50 m)
Tr[0]	4.5	0.0	66.0	4.9	0.0	99.0	Tree (% in 50 m)
Tr[1]	7.3	0.0	81.0	6.7	0.0	100.0	Tree (% in 50 m)
Tr[2]	10.3	0.0	95.0	9.5	0.0	100.0	Tree (% in 50 m)
TrD[0]	72.3	0.0	479.7	75.9	0.0	546.4	Distance to tree (m)
TrD[1]	64.9	0.0	535.6	71.8	0.0	585.0	Distance to tree (m)
TrD[2]	54.3	0.0	550.8	63.8	0.0	568.2	Distance to tree (m)
Step[0]	104.0	1.0	484.2	143.4	8.3	800.0	Daily step length (m)
Step[1]	133.3	1.0	630.3	142.8	10.7	800.0	Daily step length (m)
Step[2]	160.6	2.0	767.5	142.8	10.2	800.0	Daily step length (m)

Table 3.2. Candidate model rankings explaining patterns of northern bobwhite brood daily resource selection behavior in southwest Missouri 2016–2018, Watanabe-Akaike information criteria (WAIC), and differences in WAIC (ΔWAIC) estimating relative predictive performance of competing models. Stage-specific models evaluated differences in habitat selection patterns either across all age classes [1], between broods ≤35 and broods > 35-days old [2], or among broods 1- to 14-, 15- to 35-, and >35-days old [3]. Fitness-related models evaluated differences in habitat selection and movement patterns among broods that failed and broods that succeeded to survive to 35-days old [0|1].



Model	Rank	Variables	WAIC	ΔWAIC
Stage-specific resource selection				
	1	CA[S[3]] + Step[S[3]]	12338.2	0.0
	2	CA[S[2]] + Step[S[2]]	12374.0	35.8
	3	CA[S[1]] + Step[S[1]]	12443.5	105.2
	4	Null	13370.7	1032.4
Fitness-related resource selection				
	1	CA[0|1] + Step[0|1]	6503.4	0.0
	2	CA + Step	6505.7	2.3
	3	Null	7001.9	498.5

Notes: CA is a set of habitat covariates and includes Ag Agid Nid Nmw Ngr Npb Ngrpb Mid Mmw Mgr Mpb Sh Tr TrD - see table 3.1 for details; [S[n]] indicates habitat selection and movement parameters were evaluated for n age classes; Step indicates a daily movement variable evaluated distance travelled among empirically derived available step lengths; [0|1] indicates habitat selection and movement parameters were evaluated for broods that failed and succeeded to survive to 35-days old.

Table 3.3. Parameter estimates of full models describing habitat selection and movement decisions for northern bobwhite broods in southwest Missouri 2016–2018 breeding seasons. Mean, 2.5%, and 97.5% credible intervals, and proportion of posterior samples not overlapping zero, f, are given for each effect. Stage-specific estimates for broods ≤14 [0], 15- to 35- [1], and >35-days old [2] (left). Fate-specific estimates are for broods that survived to 35 days [1] and broods that failed to survive to 35-days old [0] (right).

	Stage [0|1|2]					Fate [0|1]			
	mean	2.5%	97.5%	f		mean	2.5%	97.5%	f
Ag[0]	0.394	0.123	0.661	0.997	Ag[0]	0.240	-0.091	0.589	0.924
Ag[1]	0.356	0.120	0.580	0.998	Ag[1]	0.382	0.063	0.691	0.989
Ag[2]	0.517	0.332	0.692	1.000					
Agid	0.252	0.112	0.377	0.999	Agid	0.206	0.027	0.370	0.985
Nid[0]	-0.159	-0.729	0.222	0.737	Nid[0]	0.259	-0.500	0.806	0.834
Nid[1]	0.161	-0.062	0.369	0.925	Nid[1]	0.082	-0.173	0.314	0.758
Nid[2]	0.362	0.050	0.634	0.986					
Ngr	0.122	-0.106	0.302	0.879	Ngr	0.101	-0.170	0.332	0.801
Npb	0.306	0.046	0.540	0.988	Npb	0.269	0.089	0.438	0.997
Npbgr	0.409	0.237	0.565	1.000	Npbgr	0.165	-0.206	0.476	0.841
Nmw	0.210	0.050	0.354	0.993	Nmw	0.365	0.145	0.592	0.999
Mid	0.044	-0.103	0.166	0.754	Mid	0.031	-0.142	0.187	0.665
Mgr	0.042	-0.152	0.188	0.726	Mgr	0.119	-0.054	0.265	0.934
Mpb	0.001	-0.275	0.190	0.565	Mpb	-0.146	-0.696	0.191	0.726
Mmw	0.292	0.152	0.423	0.999	Mmw	0.254	0.075	0.424	0.995
Sh[0]	0.017	-0.223	0.219	0.585	Sh[0]	-0.211	-0.591	0.129	0.881
Sh[1]	0.170	0.061	0.276	0.999	Sh[1]	0.189	0.039	0.319	0.992
Sh[2]	0.253	0.121	0.379	1.000					
Tr[0]	-0.065	-0.324	0.152	0.698	Tr[0]	-0.103	-0.412	0.171	0.768
Tr[1]	0.031	-0.120	0.172	0.675	Tr[1]	-0.001	-0.180	0.164	0.496
Tr[2]	-0.007	-0.177	0.150	0.526					
TrD[0]	-0.580	-0.967	-0.243	1.000	TrD[0]	-1.343	-2.294	-0.567	1.000
TrD[1]	-0.764	-1.115	-0.468	1.000	TrD[1]	-0.666	-1.023	-0.347	1.000
TrD[2]	-1.235	-1.739	-0.796	1.000					
Step[0]	-0.022	-0.048	0.004	0.953	Step[0]	0.013	-0.032	0.057	0.710
Step[1]	-0.006	-0.027	0.014	0.724	Step[1]	-0.005	-0.026	0.016	0.686
Step[2]	0.034	0.012	0.056	0.998					

Notes: Habitat parameters include agriculture (Ag), idle agriculture (Agid), idle native grassland (Nid), native grasslands that were grazed (Ngr), burned (Npb), or both (Npbgr) in the previous two years, or mowed (Nmw) in the previous 1 year, and mixed grasslands taht were idle (Mid), grazed (gr), burned (Mpb), or mowed (Mmw). Shrub (Sh) and tree (Tr) cover within 50 m, distance to tree (TrD) and daily distance travelled (Step).

FIGURES

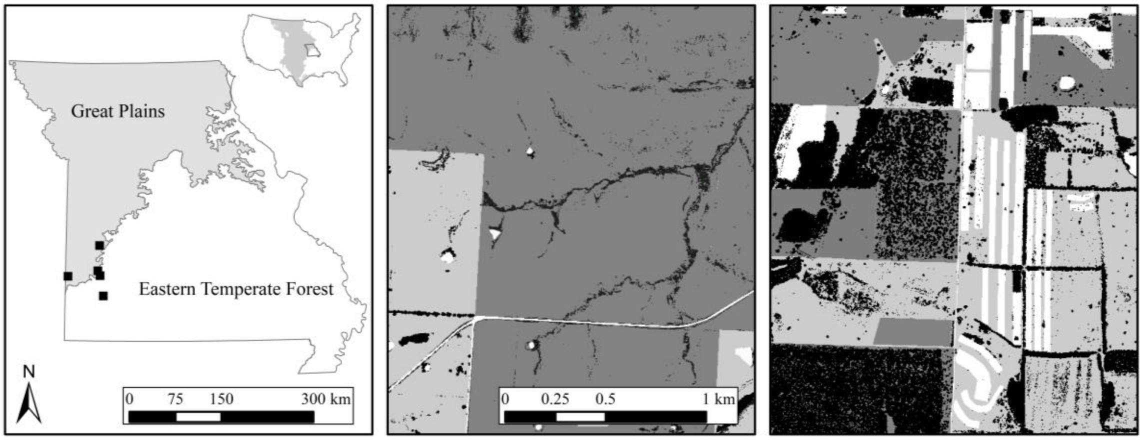


Figure 3.1. Map of study site locations on five conservation areas in southwest Missouri (left). Extensive native prairies (center) are larger continuous tracts of native grassland (■ dark grey) interspersed with shrubs and trees (■ black) and bordered by non-native grasslands (■ light grey). Intensively managed conservation areas (right) incorporate agricultural strips (□ white), woodland units and woody fencerows (■ black) within a matrix of restored native prairies (■ dark grey) and non-native mixed or cool-season grasslands (■ light grey)

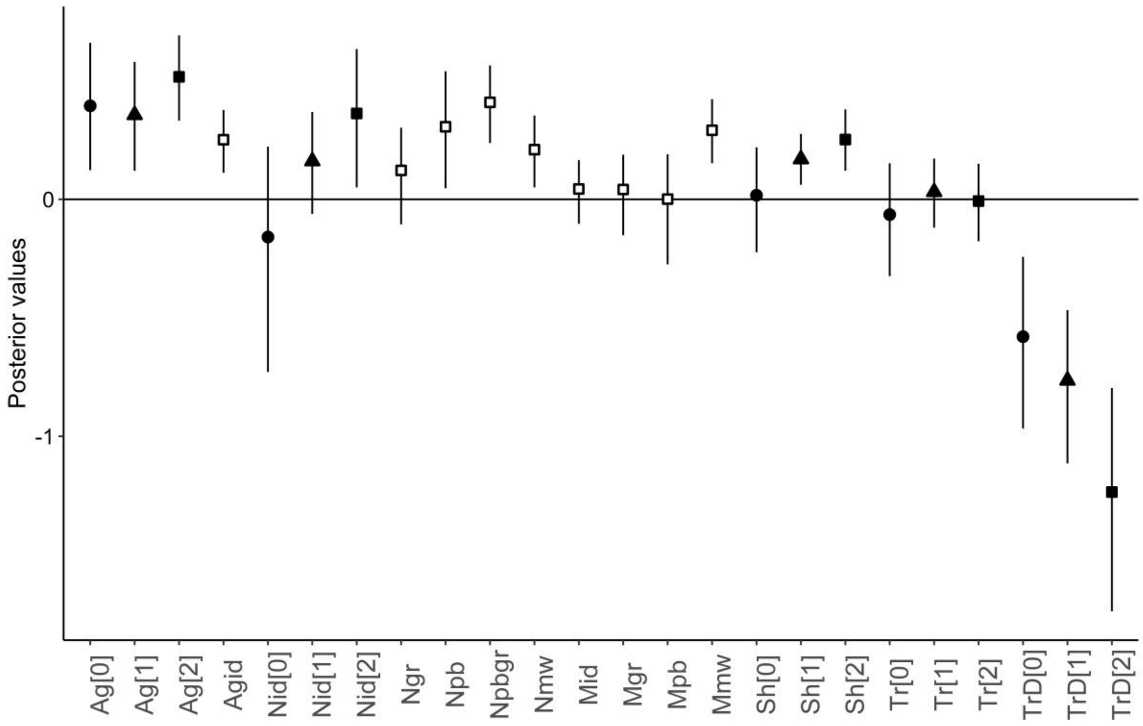


Figure. 3.2. Posterior distributions of population-level habitat selection parameters estimating utility of agricultural fields (Ag), native grasslands (N), and mixed grasslands (M) that were idle (id), grazed (gr), burned (pb), grazed and burned (pbgr), or mowed (mw), as well as brood selection for shrub (Sh) and tree cover (Tr), and selection for distance from tree (TrD) for northern bobwhite broods in southwest Missouri 2016–2018. The solid line at y = 0 represents the threshold between support for selection (+) or avoidance (-) of each habitat parameters. Stage-specific effects S[-] are presented with black mean point estimates for broods ≤14-days old [0] (●), 14- to 35-days old [1] (▲), and >35-days old [2] (■) and 95% CRI (bar). Habitat selection parameters that are stage-independent display mean point estimates in white (□) and 95% CRI (bar).

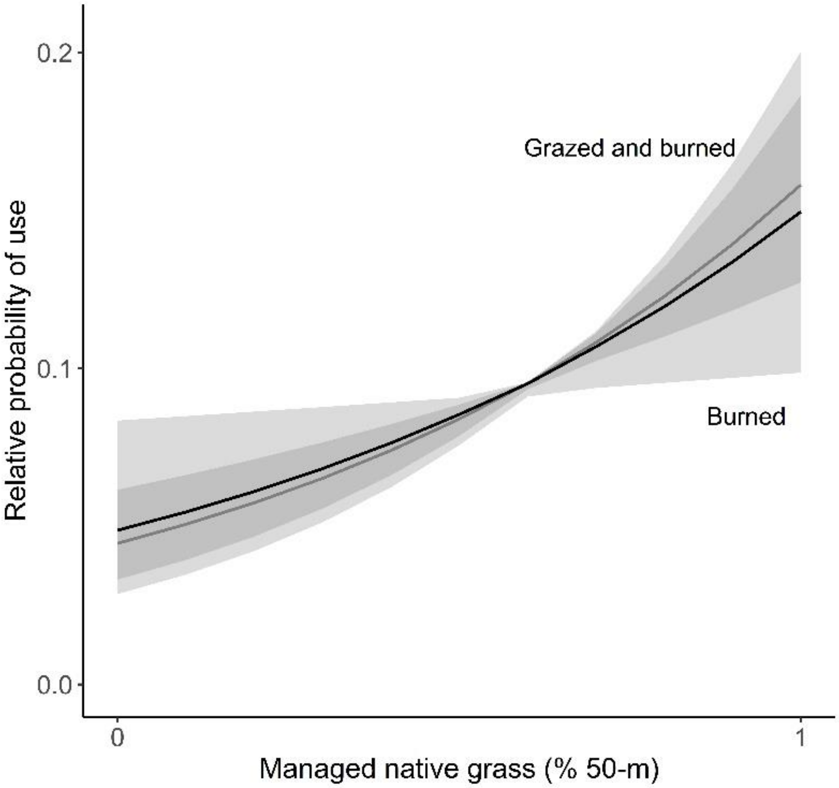


Figure 3.3. Predicted relative probability of use by northern bobwhite broods as a function of percent cover within 50 m of native grassland that was burned (black line) or both grazed and burned (grey line) within the past two years in southwest Missouri 2016–2018.

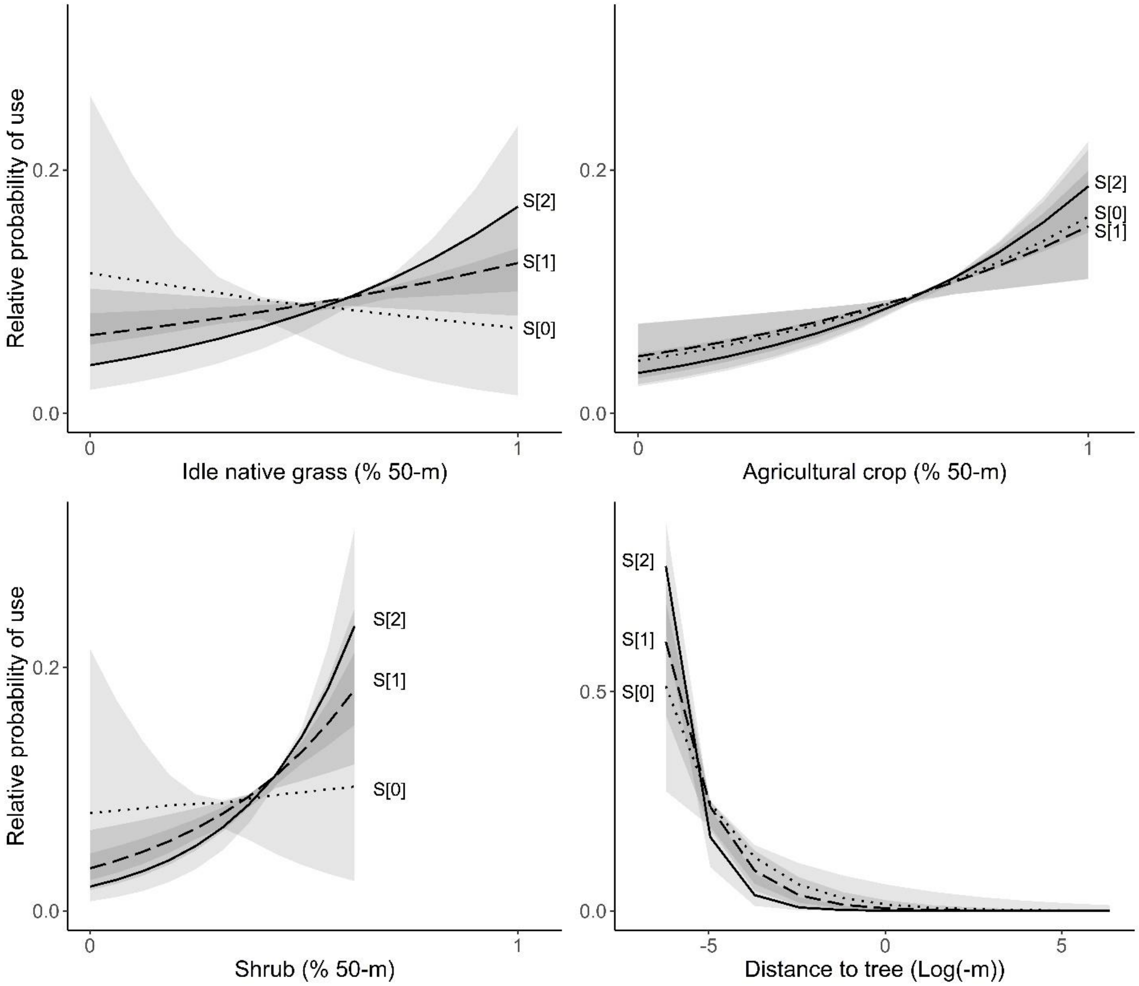


Figure 3.4. Stage-dependent predicted relative probability of use by northern bobwhite broods in southwest Missouri 2016–2018 as a function of percent cover within 50 m of idle native grassland (top left), agricultural crop (top right), and shrub cover (bottom left), and predicted relative probability of use as a function of distance to nearest tree (bottom right) for young flightless broods ≤14-days old (S[0]; dotted line), dependent broods 14- to 35-days old (S[1]; dashed line), and independent broods >35-days old (S[2]; solid line).

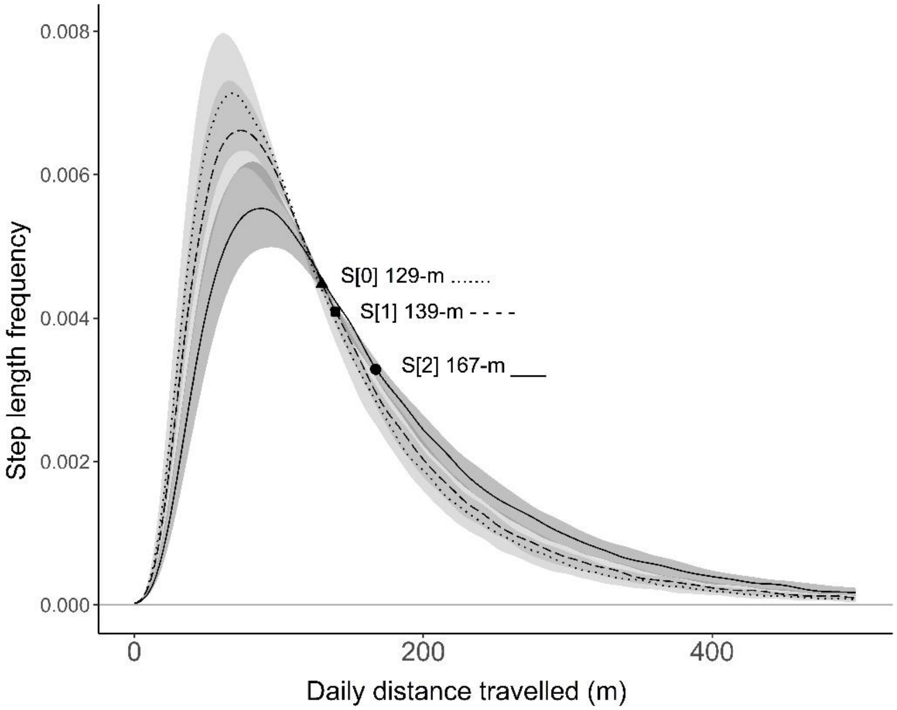


Figure 3.5. Distributions of daily distanced travelled by northern bobwhite broods in southwest Missouri 2016–2018 derived from the mean, 2.5, and 97.5% credible intervals of posterior samples of the step length parameter. Stage-specific step length distributions for broods ≤14-days old (S[0], dotted line, light grey), 14- to 35-days old (S[1], dashed line, medium grey), and >35-days old (S[2], solid line, dark grey). Mean predicted daily distance travelled for each stage are plotted with point estimates for broods ≤14-days old (●), 15- to 35-days old (▲), and >35-days old (■).

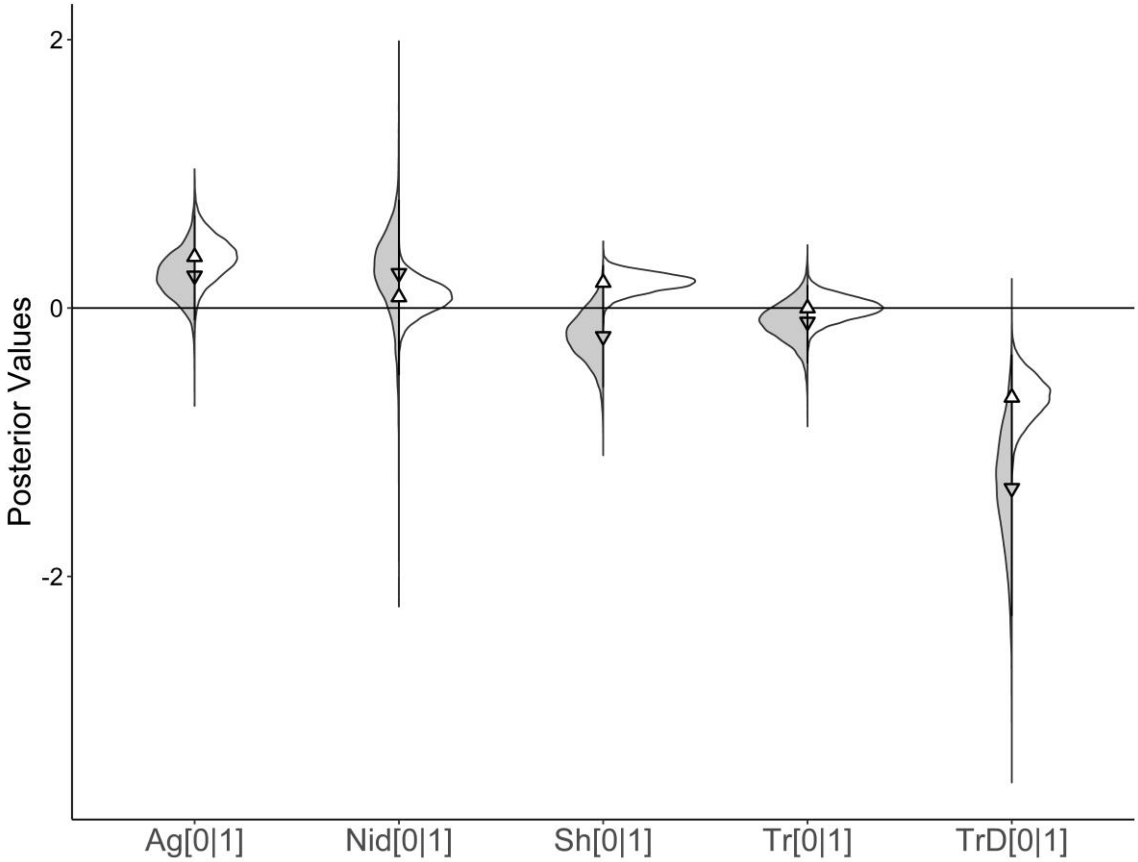


Figure 3.6. Split violin plots showing distributions of habitat parameters evaluating selection patterns of northern bobwhite broods in southwest Missouri that failed and broods that survived to 35-days old. Cover type effects for agriculture (Ag), idle native grasslands (Nid), shrub (Sh) and tree (Tr) cover, and distance to nearest tree (TrD) are presented as split violins for failed (left, grey) and successful (right, white) broods [0|1]. Means for failed broods (▲) and successful broods (∆) and 95% CRI (bar) are shown in violin plots.

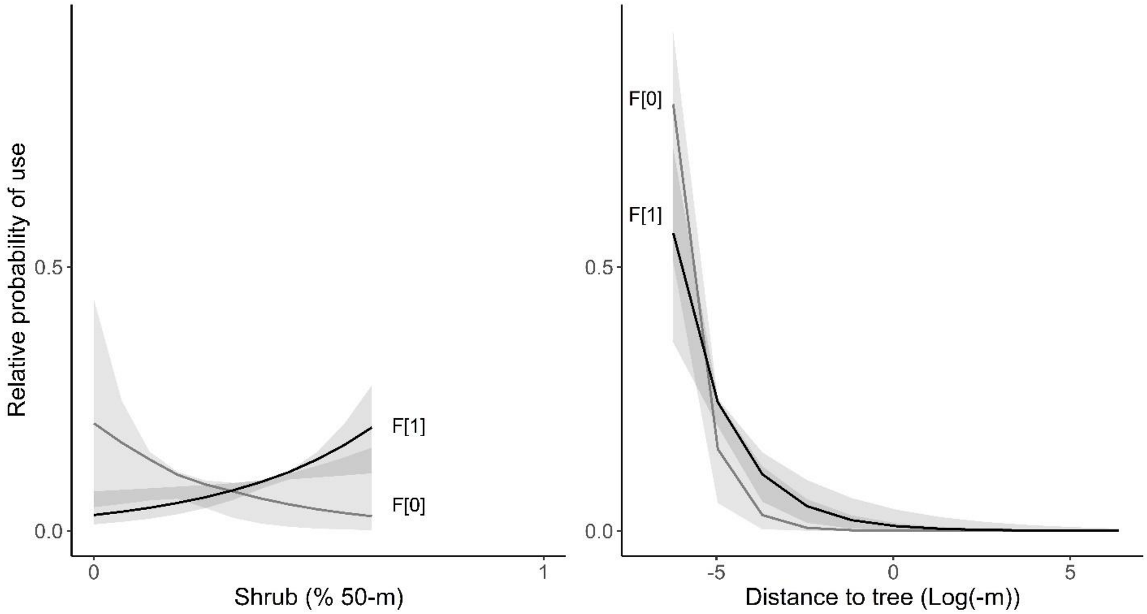


Figure 3.7. Fate-dependent predicted relative probability of use for northern bobwhite broods in southwest Missouri 2016–2018 as a function of percent shrub cover within 50 m of idle native grassland (left) and distance to nearest tree (right) for successful broods (F[1]; black line) and failed broods (F[0]; grey line).

CHAPTER 4

SEASONAL VITAL RATES AND MANAGEMENT REGIMES INFLUENCE SITE-LEVEL CHANGES IN BOBWHITE ABUNDANCE

ABSTRACT

Understanding the effects of landscape management on northern bobwhite population growth rate requires information on seasonal- and stage- specific demographic parameters. Population sensitivity to seasonal vital rates varies by region and whether a population is stable or declining. While many studies have evaluated survival, fecundity, and population growth of bobwhite populations, none have linked count, fecundity, and survival data to fully evaluate the influence of management on seasonal dynamics and population growth. Integrated population models (IPMs) allow improved estimation of vital rates across the full annual cycle through information sharing across multiple datasets. We used a two-season, two-stage, two-sex IPM to estimate population growth of bobwhite on three extensively managed sites consisting of large continuous tracts of native grassland habitat and two intensively managed sites that used traditional, fine-scale management practices such as strip crops and woody edge borders for wildlife. We evaluated effects of management and seasonal vital rates on bobwhite population growth rates on these five sites in southwest Missouri 2016–2019. Female survival was slightly lower than male survival during the breeding season ($S.b_F$ = 0.40, 95% CRI: 0.18, 0.60; $S.b_M$ = 0.44, 95% CRI: 0.23, 0.64) and juvenile survival was lower than adult survival during both breeding and non-breeding seasons ($Sjuv.b$ = 0.30, 95% CRI: 0.04, 0.59; $Sadult.b$ = 0.42, 95% CRI: 0.20, 0.62; $Sjuv.nb$ = 0.35, 95% CRI: 0.11, 0.57; $Sadult.nb$ = 0.42, 95% CRI: 0.16, 0.64). There was large inter-annual and site-level

variation in seasonal demographic rates. The number of young hatched from female-incubated nests and breeding season adult survival was greater on extensively managed sites (EMS) compared to intensively managed sites (IMS) (f_{EMS} = 4.07, 95% CRI: 2.34, 6.09; f_{IMS} = 2.38, 95% CRI: 1.11, 5.62; $Sadult.b_{EMS}$ = 0.48, 95% CRI: 0.32, 0.64; $Sadult.b_{IMS}$ = 0.33, 95% CRI: 0.18, 0.50). Non-breeding season survival was lowest on the two smallest extensively managed sites, Stony Point Prairie (960 acres) and Shelton Conservation Area (320 acres), ($S.nb_{STP}$ mean = 0.33, 95% CRI: 0.11, 0.54; $S.nb_{SLT}$ mean = 0.34, 95% CRI: 0.09, 0.58). Annual changes in pre-breeding season bobwhite abundance were most strongly correlated with non-breeding season survival (r = 0.99, 95% CRI: 0.54, 1.00), followed by variation in breeding season juvenile survival (r = 0.99, 95% CRI: 0.34, 1.00). Population growth rates for all sites indicated sharply declining trends, and the most severe declines occurred on Talbot Conservation Area (λ = 0.31, 95% CRI: 0.03, 0.65), a large intensively managed site, and on Shelton Memorial (λ = 0.37, 95% CRI: 0.00, 0.74), a small extensively managed site. Talbot's population exhibited low fecundity and breeding season adult survival. Shelton's population exhibited low breeding season juvenile survival and non-breeding season survival relative to other sites. Population growth rate was greatest on the largest extensively managed site, Wah'Kon-Tah Prairie (λ = 0.55, 95% CRI: 0.13, 0.94). Achieving stable populations requires managing for these site-level seasonal habitat needs to improve demographic rates most affecting population growth rates.

INTRODUCTION

Reversing wildlife declines requires understanding the influence of management strategies on vital rates driving population change (Bradbury et al. 2001). Population trends result from demographic and environmental processes linked across seasons and life stages (Sandercock et al. 2008). However, few studies examine multiple seasons, seasonal interactions, or the full annual cycle (Marra et al. 2015). Additionally, few studies evaluate established assumptions concerning potential influences of population structure on these dynamics. Intra-annual variation in vital rates, population structure, and linkages across seasons may contain important sensitivities affecting annual trends and population persistence. Integrated population models (IPM) provide a holistic approach for leveraging multiple data types to quantify demographic mechanisms of population change and test hypothesized drivers (Rushing et al. 2017, Arnold et al. 2018).

While population growth is a function of dependent processes occurring across seasons, research efforts have focused primarily on either the breeding season or, more recently, annual processes (Marra et al. 2015). Evaluating seasonal contributions to annual dynamics is critical for management of species with seasonally-specific threats (Hostetler et al. 2015, Villellas et al. 2015). These threats may include changes in predator communities, habitat disturbances, or weather patterns. Evaluating seasonal dynamics within an annual framework also accounts for carry-over effects, when processes that occurred in one season explain reproductive success or survival in a subsequent season (Harrison et al. 2011). For example, quality of non-breeding season habitat or pre-breeding season weather events may influence body condition and reproductive success of breeding birds (Gunnarsson et al. 2005, Robson and Barriocanal

2008). These intra-annual processes driving annual dynamics can be accounted for in a periodic population model to better understand temporal variation in vital rates regulating population growth (Hunt and Tongen 2016, Rushing et al. 2017).

Population age-structure and composition may also affect the contribution of vital rates to population growth. While models often incorporate age-structured demographic information, they rarely account for male and female composition. Single-sex, female-based population models assume either (1) sexes exhibit similar vital rates, or (2) female dynamics drive population change (Caswell et al. 1986). Several circumstances may violate these assumptions and generate misleading results concerning population growth, elasticity, and extinction risk (Gerber and White 2014). Male and female survival may differ due to behavioral and environmental interactions (Caswell et al. 1986). In species where males either contribute to or limit reproductive success, biased sex ratios may influence annual fecundity rates, violating the assumption of female dominance (Caswell et al. 1986, Gerber and White 2014). Two-sex population models are necessary to evaluate population viability where vital rates differ between males and females and where sex ratios may be skewed or vary due to those differences (Caswell et al. 1986, Gerber and White).

IPMs are a flexible, robust framework to evaluate influences of seasonal population demographics and structure on annual growth rates and sensitivity. Within an IPM, survival, fecundity, and abundance patterns are described by individual data sets and likelihood functions to explicitly account for processes underlying population change (Schaub et al. 2007, Zipkin and Saunders 2018). These individual likelihood functions are linked to formulate a joint likelihood, whereby information sharing across multiple sources leads to a holistic evaluation of population dynamics. IPMs can be used to link seasonal vital rates, estimate annual population growth, and evaluate the influence of habitat management strategies on demographic sensitivities of species of conservation concern (Rushing et al. 2017).

Northern bobwhite (*Colinus virginianus*; hereafter bobwhite) population declines began as early as 1880 (Leopold 1931). Bobwhite abundance in Missouri has been reduced by 80% since 1967 and this rate of loss has accelerated over the past 15 years (Sauer et al. 2017). Bobwhite declines are largely explained by habitat loss, fragmentation, and degradation (Brennan 1991, Veech 2006, Williams et al. 2004, Hernandez et al. 2013). Local exceptions to rangewide declines occur on landscapes purposefully managed for bobwhite (McConnell et al. 2018). Bobwhite are a year-round resident that completes their full life cycle on a single landscape, but are exposed to seasonally-specific threats (Stoddard 1931, Brennan et al. 2014). Recovery on an altered landscape requires a better understanding of conservation and management strategies on full-annual cycle dynamics. Traditional, fine-scale management practices incorporating windbreaks, field borders, and agricultural strip crops have been applied to many public and private lands for habitat improvement (Williams et al. 2004). The conservation efficacy of these traditional strategies applied on intensively managed sites relative to management of native habitats, such as grasslands on extensively managed sites, has not been evaluated.

The Missouri Department of Conservation (MDC) initiated a large-scale effort to recover the state’s bobwhite populations in areas with the best potential for recovery (MDC 2016). An MDC bobwhite strategic plan identified landscape management as a research priority for conservation efforts. MDC in partnership with University of Missouri established the southwest quail study to evaluate survival, productivity, and abundance across the full annual cycle on five conservation areas employing two general management approaches. Robert E. Talbot and Shawnee Trail Conservation Areas are intensively managed sites that incorporate small units (2–60 acres) of agriculture and woody vegetation among grassland units to provide food and cover for wildlife. Shelton Memorial Conservation Area, Stony Point Prairie Conservation Area, and Wah'Kon-Tah Prairie are extensively managed sites having large continuous tracts of native grassland habitat maintained with fire, grazing, and mowing practices.

Our objectives were to develop a two-season, two-sex, age-structured integrated population model to: (1) evaluate effects of public lands management strategies on population growth, and (2) identify seasonal- and sex-specific demographic rates driving population change. We hypothesized bobwhite fecundity, survival, and population growth rates would be greater on extensively managed sites compared to intensively managed sites. Extensively managed sites, having native grassland communities and rotational disturbance regimes, may provide bobwhite a mosaic of habitats suitable for nesting, brood-rearing, foraging, and cover throughout the year. By contrast, agricultural units on intensively managed sites may not provide nesting habitat or year-round usable space for bobwhite. Also, mature linear tree edges on intensively managed sites may also reduce survival and nesting success by creating perches and habitat for predators. We also hypothesized population growth rate would be most correlated with non-breeding season survival and breeding season survival of adults and young hatched (Folk et al. 2007, Sandercock et al. 2008, Gates et al. 2012, Williams et al. 2012). However, nest success and other factors affecting fecundity and recruitment may also be important (Folk et al. 2007, Gates et al. 2012, McConnell et al. 2018).

METHODS

Study Area

We estimated seasonal-, age-, and sex-specific survival and fecundity; and abundance and population growth for bobwhite on five conservation areas in the eastern tallgrass prairie of southwest Missouri from 1 May 2016 to 1 May 2019. This region has been heavily modified by agriculture, but it has also been identified by the National Bobwhite Conservation Initiative as having high potential for bobwhite recovery (NBCI 2011). Our study area included two intensively managed sites–Shawnee Trail (3635 acres) and Robert E. Talbot Conservation Areas (4361 acres; Fig. 4.1.A) and three extensively managed sites–Shelton Memorial Conservation Area (320 acres), Stony Point Prairie Conservation Area (960 acres), and Wah'Kon-Tah Prairie (3030 acres; Fig. 4.1.B).

Survival, fecundity, and abundance data

We collected survival, fecundity, and abundance data on our five study sites beginning in February each year 2016–2018 in cooperation with MDC. Bobwhite were captured using funnel traps in February and March and fitted with uniquely numbered leg bands and 6 g necklace style radio-transmitters (model AWE-QII from American Wildlife Enterprises, Monticello, FL, USA). Radio-marked adult bobwhite were tracked at least three times per week to monitor adult breeding season survival. Success of nests incubated by radio-collared birds were monitored to estimate the number of eggs hatched per adult as a measure of fecundity. Broods of radio-tagged adults were captured at around 20-days old and fitted with backpack transmitters to estimate juvenile breeding season survival (Chapter 2). We used Funnel traps in October of each year, to capture, band, and radio-tag adults and juveniles for non-breeding season survival estimates (see Mosloff 2020 for details).

MDC conducted bobwhite spring whistle counts 15 May–1 July, 2016–2018 on Shawnee Trail (*n* = 16 listening stations), Shelton Memorial (*n* = 2), Stony Point Prairie (*n* = 8), Robert E. Talbot Conservation Area (*n* = 16), and Wah'Kon-Tah Prairie (*n* = 18). The number of birds calling within 500 m were recorded during a 10-min period between sunrise and 9:00 A.M during 1–3visits to each station. We summed the number of bobwhite heard calling at all listening stations during a visit and selected the maximum heard during one round of surveys as our index of pre-breeding season abundance.

Integrated population model

We linked spring whistle counts with nest monitoring and telemetry data within an IPM (Besbeas et al. 2002, Schaub et al. 2007, Schaub and Abadi 2011, Kéry and Schaub 2012). Models of survival, productivity, and population size are linked by common parameters. We used a two-stage, two-sex periodic matrix design to account for important seasonal demographic complexities across the full annual cycle. Our periodic matrix model allowed us to explicitly account for seasonal processes important in understanding intra-annual demographic sensitivities (Guthery et al. 2000, Doak and Morris 2010, Villellas et al. 2015, Hunt and Tongen 2017). We estimated demographic rates during both the breeding season (1 May–31 Oct) and non-breeding season (1 Nov–

30 Apr). Our two-stage, two-sex matrix structure accounted for differences in survival and productivity among groups of adults and juveniles and males and females (Sandercock et al. 2008). We included sex-specific productivity rates because bobwhite are polygamous, and both females and males contribute to fecundity as nest-incubating and brood-attending adults (Caswell and Weeks 1986, Curtis et al. 1993, Burger et al. 1995ab, Gerber and White 2014). We fit our IPM in a Bayesian framework with a joint likelihood and prior probability distributions for estimates of abundance, survival, and productivity.

Count likelihood

We estimated change in population size for each year *t* at each site j for males and females *k* within a state-space model. Spring whistle count data $C_{t,j,k}$ were described in a Poisson regression as part of the observation process (Eq. 1). We assumed an even male-female sex ratio and doubled the number of males heard whistling across each site and year for an index of total pre-breeding season abundance. The true, but unknown population size $N_{t,j,k}$ was described in a system-process equation (Eq. 2). This true population size was the sum of two annual processes: (1) the number of adults from the previous year $Nadult_{t,j,k}$ that survived breeding season ($Sadult.b_{t,j,k}$) and non-breeding season ($Sadult.nb_{t,j,k}$), estimated as the outcome of a binomial distribution (Eq. 3), and (2) the number of juveniles produced $f_{t,j,k}$ that survived that same period ($Sjuv.b_{t,j,k}, Sjuv.nb_{t,j,k}$) estimated as the outcome of a Poisson distribution (Eq. 4). Population growth rate $\lambda_{t,j}$ was derived from abundance estimates across age classes, males, and females (Eq. 5).

$C_{t,j,k} \sim pois(Nadult_{t,j,k} + Njuv_{t,j,k})$ Count observation process (1)

$N_{t,j,k} = Nadult_{t,j,k} + Njuv_{t,j,k}$ Abundance state process (2)

$Nadult_{t,j,k} \sim bin(Sadult.b_{t-1,j,k} * Sadult.nb_{t-1,j,k}, Nadult_{t-1,j,k})$

Adult abundance (3)

$Njuv_{t,j,k} \sim pois(f_{t-1,j,k} * Sjuv.b_{t-1,j} * Sjuv.nb_{t-1,j,k})$ Juvenile abundance (4)

$\lambda_{t,j} = \frac{N_{t,j}}{N_{t-1,j}}$ Population growth (5)

Survival data and analysis

We incorporated three known-fate logistic exposure likelihoods in our IPM to estimate seasonal, age-, and sex-specific survival (Eq. 6). This generalized linear mixed model included a modified link function, which allowed interval length between survival observations (*d*) to vary without biasing estimates of daily survival (Eq. 7; Shaffer and Thompson 2007). These three likelihoods included (1) breeding season juvenile survival, (2) breeding season adult survival, and (3) non-breeding season survival. All models estimating daily survival $p_{t,j,k,l}$ included additive fixed effects for year β_t, and site β_j (Eq. 8). The breeding and non-breeding season adult survival models included a fixed binary effect for sex β_k. The breeding season juvenile survival model included a fixed quadratic effect for brood age in days and the non-breeding season survival model included a fixed binary age effect for adults and juveniles β_l. Each of the three models also included a unique intercept term α. We assigned vague priors for all fixed effects and intercepts (ex. $\beta_k \sim normal(0, 0.001)$). The logistic-exposure generalized-linear mixed model for non-breeding season adult survival ($Sadult.nb_{t,j,k,l}$) can be written mathematically as:

$Sadult.nb_{t,j,k,l} \sim bernoulli(p_{t,j,k,l})$ Distribution of daily survival (6)

$p_{t,j,k,l} \sim s^{d}_{t,j,k,l}$ Modified link function (7)

$\log(s_{t,j,k,l}) = \beta_t + \beta_j + \beta_k + \beta_l + \alpha$ Linear predictor of survival (8)

Productivity data and analysis

We defined fecundity $f_{t,j,k}$ as the number of eggs hatched each year *t* at each site *j* per female or male *k*. We estimated fecundity using nest monitoring observations of the total number of eggs hatched by females and the total number of eggs hatched by males $J_{t,j,k}$ across all adults active on 1 May each year for each site $R_{t,j,k}$ (Eq. 9, Eq. 10).

$$J_{t,j,k} \sim pois(\rho_{t,j,k}) \tag{9}$$

$$\rho_{t,j,k} = R_{t,j,k} f_{t,j,k} \tag{10}$$

Population projection

While we had count and demographic data for 2016 through 2018, we projected bobwhite abundance and population change for 2019 by sampling from the posterior distribution of our 2018 demographic rates and estimated abundances (Kéry and Schaub 2012, Oppel et al. 2014).

We fit our IPM in a Bayesian framework in Program R version 3.6.1 using JAGS via the JagsUI package (R Core Development Team 2019, Plummer 2003, Kellner 2019). We evaluated model convergence by inspecting trace plots for all parameters and checking for Rhat statistic values of <1.1 (Kéry and Schaub 2012). We present posterior means and 95% credible intervals (CRI) of estimated parameters and demographic rates. Effects whose credible intervals did not overlap zero were interpreted as influential. We also calculated correlation coefficients between demographic rates and population growth (r) and the probability a demographic rate positively influences population growth ($P(r>0)$) as a measure of demographic sensitivity to seasonal vital rates.

RESULTS

We tracked 766 juveniles and 618 adults during the breeding season, and 772 juveniles and 349 adults during the non-breeding season to estimate survival. We monitored success of 276 nests incubated among 576 adults active on 1 May at the start of the breeding season across all years. MDC conducted three rounds of bobwhite spring whistle counts on Shawnee Trail, Shelton Memorial, and Stony Point Prairie annually 2016–2018, two rounds on Robert E. Talbot Conservation Area in 2017, and, on Wah'Kon-Tah Prairie, three rounds of spring whistle counts were conducted in 2016 and two in 2017 and 2018.

Bobwhite exhibited highly variable seasonal, annual, and site-level survival and fecundity rates from 2016 through 2018 (Fig. 4.2; Table 4.1). During the breeding season, female-incubated nests hatched almost 4 times the number of young as male-incubated nests across all sites and years (f_F = 3.40, 95% CRI: 1.25, 5.96; f_M = 0.89, 95% CRI: 0.00, 2.85; Table 4.1). There was weak support that adult female breeding season survival ($Sadult.b_F$ = 0.40, 95% CRI: 0.18, 0.60) was lower than adult male breeding season survival ($Sadult.b_M$ = 0.44, 95% CRI: 0.23, 0.64; β_{male}= 0.13 , 95% CRI: -0.09 to 0.35;

Table 4.1). In line with our hypotheses, female fecundity was higher on extensively managed sites (*Ext*) compared to intensively managed sites (*Int;* f_{Ext} = 4.07, 95% CRI: 2.34, 6.09; f_{Int} = 2.38, 95% CRI: 1.11, 5.62; Fig. 4.2, Fig. 4.3), as were adult during the breeding season ($Sadult.b_{Ext}$ = 0.48, 95% CRI: 0.32, 0.64; $Sadult.b_{Int}$ = 0.33, 95% CRI: 0.18, 0.50; Fig. 4.2, Fig. 4.3, Table 4.1). Talbot had the highest mean rate for breeding season juvenile survival, ($Sjuv.b_{TAL}$= 0.38, 95% CRI: 0.13, 0.63) while Shelton Memorial had relatively low breeding season survival ($Sjuv.b_{SLT}$ = 0.18, 95% CRI: 0.02, 0.41; Table 4.1).

During the non-breeding season, juvenile survival was lower than adult survival, as predicted, and these differences were nearly credible ($Sjuv.nb$ = 0.35, 95% CRI: 0.11, 0.57; $Sadult.nb$ = 0.42, 95% CRI: 0.16, 0.64; β_{ad}= 0.20, 95% CRI: -0.11, 0.23; Table 4.1). We found no substantial difference in survival between sexes. We found a credible difference in non-breeding season survival across years; survival probabilities were highest in 2017, and lowest in 2018 across all sexes and age classes ($S.nb_{2016}$ = 0.41 , 95% CRI: 0.25, 0.57; $S.nb_{2017}$ = 0.50 , 95% CRI: 0.33, 0.65; $S.nb_{2018}$ = 0.24 , 95% CRI: 0.09, 0.42; Fig. 4.2). While we predicted non-breeding season survival would be greater on extensively managed sites, we found mean survival was higher across intensively managed sites ($S.nb_{Ext}$ = 0.36 , 95% CRI: 0.11, 0.59; $S.nb_{Int}$ = 0.42 , 95% CRI: 0.16, 0.64; Fig. 4.3). Variation around mean non-breeding survival was greater than variation around those during the breeding season (Fig. 4.3). Shawnee Trail, an intensively managed site, had the highest mean non-breeding season survival across all years, age-classes, and sexes ($S.nb_{SHT}$ mean = 0.45, 95% CRI: 0.20, 0.65), followed by the largest extensively managed site, Wah'Kon-Tah ($S.nb_{WKT}$ mean = 0.41, 95% CRI:

0.17, 0.61; Fig. 4.2, Fig. 4.3, Table 4.1). The two smaller native grassland sites, Stony Point Prairie and Shelton Memorial had the lowest non-breeding season survival across all years, age-classes, and sexes ($S.nb_{STP}$ mean = 0.33, 95% CRI: 0.11, 0.54; $S.nb_{SLT}$ mean = 0.34, 95% CRI: 0.09, 0.58; Fig. 4.2, Fig. 4.3, Table 4.1).

Spring whistle counts showed declining trends for all sites with 3 consecutive years of survey data 2016–2018 (Fig. 4.4, Table 4.2). All field counts were within the 95% credible range of male abundance estimates except for Shawnee Trail 2018, which was estimated low (Table 4.2). We predicted population growth rate would be greater on native grassland sites compared to areas that incorporated traditional, fine-scale management practices. We found mean population growth rate was highest on the largest extensively managed site, Wah'Kon-Tah (λ_{WKT} = 0.55, 95% CRI: 0.13, 0.94) and lowest on Talbot Conservation Area, an intensively managed site (λ_{TAL} = 0.31, 95% CRI: 0.03, 0.65; Table 4.1).

We calculated correlations between each demographic rate and population growth to evaluate the relationship between variation in seasonal vital rates with changes in annual abundance (Kéry and Schaub 2012). As predicted, non-breeding season survival had the strongest correlation with population growth rate for both age classes and sexes ($r_{S\ juv.nb}$= 0.99 (95% CRI: 0.54, 1.00), $r_{S\ adult.nb}$= 0.99 (95% CRI: 0.55, 1.00); Fig. 4.6). Breeding season juvenile survival also had a credible, positive correlation with population growth ($P(r>0)$ = 0.99; Fig. 4.3, Table 1). Contrary to our predictions, we did not find a strong correlation between population growth rate and breeding season adult fecundity or survival (Fig. 4.5, 4.6).

DISCUSSION

Variation in bobwhite non-breeding season survival (1 November to 30 April) explained the most variation in population growth rate, followed by breeding season juvenile survival. We also found females hatched more young and adult breeding season survival was higher on extensive native grassland sites compared to intensively managed sites. Bobwhite population growth rates were well below 1 at all sites, suggesting large population declines in the years of our study. Vital rates were highly variable across sites and years and posterior samples of those that resulted in stable populations (population growth rate ≥1) suggested much higher minimum non-breeding season survival and average breeding season survival and fecundity rates are needed across sites to achieve population stability (Fig. 4.3).

Non-breeding season survival

Bobwhite face multiple pressures during the non-breeding season. Previous field, simulation, and meta-analysis studies have similarly found non-breeding season survival contributes disproportionately to abundance trends, especially for northern populations of bobwhite (Guthery et al. 2000, Folk et al. 2007, Sandercock et al. 2008, Link et al. 2008, Gates et al. 2012, Williams et al. 2012).

Stochastic or extreme winter weather may lead to greater risk of exposure, predation, or starvation (Errington 1936, Roseberry and Klimstra 1984). Snow accumulation reduces local survival and correlates with regional declines in abundances over multiple years (Janke et al. 2017). While Missouri’s climate is similar to that experienced by other northern populations of bobwhite, winter weather during our field study was mild and our populations likely did not experience anomalous events we would predict would reduce winter survival or annual population growth (Janke et al. 2017). Monthly averages of daily and minimum temperatures as well as monthly cumulative precipitation on our sites during the study period were not colder or wetter than local 30-year averages (Table 4.3; Missouri Mesonet, PRISM). Quantifying population-level effects of severe winter weather on abundance and growth rates would require long-term data to capture variation in Missouri's winter climate.

Population density, covey dynamics, and landscape composition may have influenced our observed non-breeding season survival patterns. Small coveys, especially in low density populations, experience reduced winter survival if they remain isolated or are required to make large movements to find additional members (Williams et al. 2003a, Williams et al. 2003b, Williams et al. 2000, Janke et al. 2013). Shelton Memorial is the smallest conservation area we studied (320 acres), isolated by row crops, and has among the lowest observed densities of any of our sites (Ripper et al. 2018). We found Shelton also had the lowest estimated non-breeding season survival across our 3-year study period (Table 4.1).

Habitat composition, management, and hunting pressure may also interactively influence winter survival. During this period bobwhite benefit from grassland landscapes that provide permanent cover with ample shrubby vegetation (Williams et al. 2000, Janke et al. 2015, Mosloff 2020). Hence, we would expect winter survival to be highest on our larger native grassland sites with patchy woody cover. However, survival was highest on Shawnee Trail, an intensively managed site, followed by Wah'Kon-Tah Prairie. Stony Point Prairie and Shelton had low estimated non-breeding season survival. For some populations hunting may be additive to natural predation, especially when selection for woody cover increases harvest mortality (Williams et al. 2000, Williams et al. 2003b). More data are needed to assess effects of hunting pressure on our study sites; hunting pressure was assumed to be low on most areas but this may not be the case.

Our results would also benefit from further evaluation of survival during transitional periods between the breeding and non-breeding seasons. We do not yet know if our non-breeding season survival patterns are driven by winter processes (1 Nov–28 Feb) or changes occurring in spring (1 Mar–30 April) when coveys break up and individuals set out to establish territories. As individuals disperse from groups in early spring, they may be more vulnerable to variable temperatures and rainfall or predation due to loss of group vigilance, hawk migration, or breeding displays.

We found non-breeding season survival was highly variable ($S.nb_{observed}$ = 0.38 , 95% CRI: 0.12, 0.61), while posterior estimates that resulted in population growth rates ≥1.0 had higher mean and minimum 6-month period survival ($S.nb_{stable}$ = 0.46 , 95% CRI: 0.33, 0.59; Fig. 4.4). Achieving greater minimum non-breeding season survival would improve population viability (Sandercock et al. 2008).

Breeding-season juvenile survival

Juvenile survival during the breeding season was also strongly correlated with annual changes in bobwhite abundance. Breeding season juvenile survival had the highest level of variation among survival estimates across years for each site (Table 4.1). Long-term capture-recapture data from a stable population at Tall Timbers Research Station in Florida estimated a 100-day period survival of 0.32 (95% CI: 0.18, 0.44; Terhune et al.

2019). Breeding season juvenile survival at all of our sites in southwest Missouri overlap those estimated at Tall Timbers. However, our site-level estimates have greater variation than those at Tall Timbers and our estimate of mean breeding season juvenile survival at Shelton Memorial Prairie (mean = 0.18, 95% CRI: 0.02, 0.41) is much lower than Tall Timbers. Precocial young are vulnerable to stochastic weather patterns during their early development, especially precipitation (Spiers et al. 1985, Terhune et al. 2019). Survival is also sensitive to amount and suitability of habitat, cover type, and local management practices survival (Tanner et al. 2019, Chapter 2). Reducing annual variation in juvenile survival and increasing mean survival by establishing shrub cover and applying rotational burning and grazing practices on native grassland habitats should benefit annual population trends.

Breeding-season fecundity and adult survival

As an r-selected species with low annual survival, we expected fecundity rates to influence population growth rate (Sæther and Bakke 2000, Stahl and Oli 2006, Folk et al. 2007, Gates et al. 2012, Taylor et al. 2012). However, we found no correlation between changes in abundance and the number of eggs hatched from female- and male-incubated nests. These results are actually consistent with established theory given observed population trajectories in southwest Missouri. Fecundity may explain variation in stable populations of r-selected species, but survival has a stronger influence for declining populations (Meats 1971, Sandercock et al. 2008, McConnell et al. 2018). The flexible mating system in bobwhite maximizes potential reproductive output, however nest survival, probability of renesting and double brooding, as well as male nesting rates are not strongly correlated with population change in field studies (Curtis et al. 1993, Burger et al. 1995b, Sandercock et al. 2008). Yet, successful recruitment to next year's population is important for maintaining stable populations (McConnell et al. 2018).

Adult breeding season survival did not appear to be an important determinant of population growth in southwest Missouri during our study period, however other populations are sensitive to adult summer survival (Sandercock et al. 2008, Gates et al. 2012, Williams et al. 2012). While adult breeding season survival in southwest Missouri was not strongly correlated with population growth rates, estimates for each site were less variable across years than non-breeding season survival and breeding season estimates were higher on extensively managed sites compared to intensively managed sites.

Management clearly affected fecundity and breeding season adult survival, unlike other vital rates. We found females hatched more young on extensively managed sites compared to intensively managed sites. Adult survival for both males and females was also higher on those extensively managed sites. Our results suggest these traditional, fine-scale practices designed to maximize quail populations on less acreage do not support vital rates that contribute to fall populations (Leopold 1933, Williams et al. 2004).

Annual population growth and bobwhite management

We found changes in annual abundance were the product of multiple effects associated with management strategies, seasonal demographic variation, and site characteristics. Greater fecundity and adult breeding season survival on native grassland sites did not directly correlate with greater annual population growth rates because both intensively managed sites had higher mean non-breeding season survival than the two smaller extensively managed sites, Shelton Memorial and Stony Point. Juvenile breeding-season survival was correlated with population growth but it varied greatly among sites and there was no clear difference between extensively and intensively managed sites. However, we found that juvenile survival was positively related to the amount of grazed and burned native grassland surrounding brood locations on these sites (Chapter 2). Seasonal vital rates of subpopulations at each of the five sites were quite different, indicating site-specific dynamics affected by local management, local threats and environmental influencers are important drivers of regional population declines (Coates et al. 2018).

Our population growth estimates were well below those required for stable populations. While telemetry-based estimates may be biased low due to tagging effects on marked individuals (Guthery and Lusk 2004), seasonal demographic rates were within the range of previous studies, many of which investigated declining populations (Sandercock et al. 2008, Janke et al. 2017, McConnell et al. 2018). Our estimated rates may be realistic given the highly variable nature of bobwhite demographics, which can be characterized by prolonged periods of decline and growth even in stable populations (McConnell et al. 2018). The IPM framework may also buffer any potential negative tagging effects by sharing information across abundance, fecundity, and survival datasets in the joint likelihood. Furthermore, overlap in observed counts and abundance estimates provide substantial verification of vital rate estimates. Long-term monitoring of these bobwhite populations would be needed for a robust assessment of population viability.

Northern bobwhite populations in southwest Missouri exhibited site-specific differences in seasonal vital rates. Extensive native grassland management supported greater fecundity and adult survival than fine-scale, intensive-management practices.

However, achieving population stability will require greater non-breeding season survival and breeding season juvenile survival. Small habitat islands, such as Shelton Memorial, are also more vulnerable to decline and subsequently local extinction. They may be too small to consider as a focus for quail management at a local scale. More research needs to be conducted to investigate how different landscapes (>3 km^2) incorporating both multiple and/or large public and private lands can influence long term viability and stability of bobwhite populations in Missouri.

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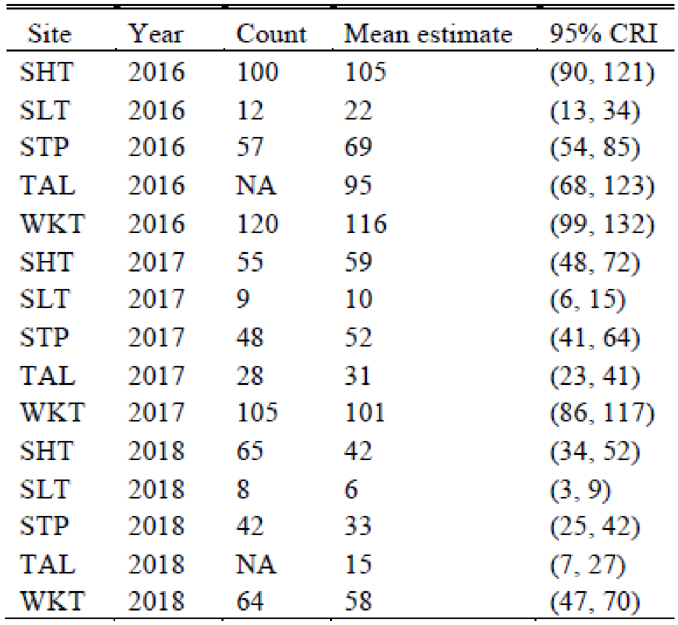
TABLES

Table 4.1. Posterior means and 95% credible intervals of estimated population growth and demographic rates for northern bobwhite populations at each site in southwest Missouri 2016–2018. Shawnee Trail (SHT) and Talbot (TAL) Conservation Areas are intensively managed sites. Stony Point Prairie (STP), Shelton Memorial Conservation Area (SLT), and Wah'Kon-Tah Prairie (WKT) are extensively managed sites.

	SHT	SLT	STP	TAL	WKT
λ	0.51 (0.15, 0.78)	0.37 (0.00, 0.74)	0.51 (0.08, 0.85)	0.31 (0.03, 0.65)	0.55 (0.13, 0.94)
f_F	2.77 (1.02, 5.83)	3.58 (1.94, 5.09)	4.70 (3.09, 6.40)	2.00 (1.26, 2.78)	3.94 (2.59, 5.79)
f_M	0.34 (0.00, 1.21)	1.07 (0.00, 3.15)	1.42 (0.30, 3.08)	1.10 (0.40, 1.92)	0.52 (0.00, 1.22)
$Sjuv.b$	0.37 (0.12, 0.62)	0.18 (0.02, 0.41)	0.31 (0.09, 0.55)	0.38 (0.13, 0.63)	0.28 (0.07, 0.51)
$Sadult.b_F$	0.36 (0.25, 0.49)	0.42 (0.28, 0.57)	0.42 (0.30, 0.54)	0.24 (0.15, 0.36)	0.53 (0.42, 0.64)
$Sadult.b_M$	0.41 (0.29, 0.53)	0.47 (0.32, 0.61)	0.47 (0.35, 0.58)	0.29 (0.19, 0.40)	0.57 (0.47, 0.68)
$Sjuv.nb_F$	0.41 (0.17, 0.59)	0.29 (0.07, 0.52)	0.29 (0.08, 0.47)	0.34 (0.11, 0.54)	0.36 (0.14, 0.55)
$Sjuv.nb_M$	0.43 (0.19, 0.61)	0.31 (0.08, 0.54)	0.30 (0.10, 0.49)	0.36 (0.13, 0.56)	0.38 (0.16, 0.57)
$Sadult.nb_F$	0.48 (0.24, 0.66)	0.36 (0.12, 0.59)	0.36 (0.13, 0.55)	0.41 (0.17, 0.61)	0.43 (0.20, 0.62)
$Sadult.nb_M$	0.50 (0.26, 0.67)	0.38 (0.13, 0.60)	0.37 (0.15, 0.57)	0.43 (0.18, 0.63)	0.45 (0.22, 0.64)

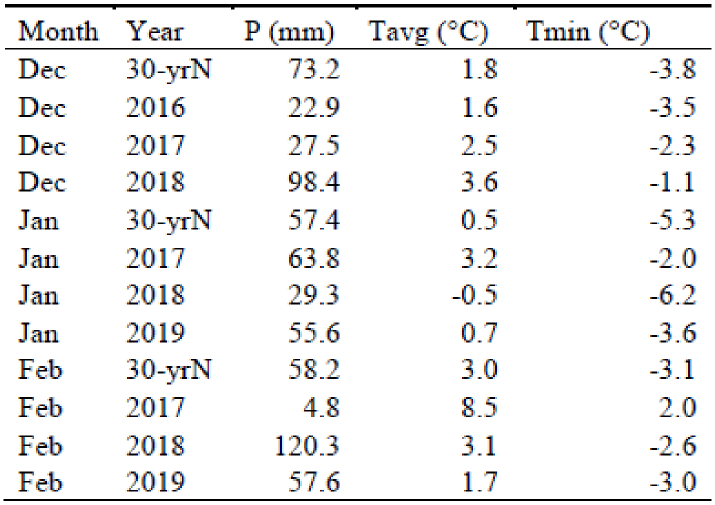
λ population growth; *f* number of young hatched from female-incubated nests F, and male incubated nests M; 6-month periodsurvival (S) for juveniles (juv), adults (adult), females (F), and males (M), during the breeding season (b), and non-breeding season (nb).

Table 4.2. Counts of male northern bobwhite heard whistling during spring surveys, posterior means and 95% credible intervals of IPM-estimated site-level male abundances at Shawnee Trail SHT, Shelton Memorial SLT, Stony Point Prairie STP, Talbot Conservation Areas TAL, and Wah’Kon-Tah Prairie WKT 2016–2018 in southwest Missouri.



Site	Year	Count	Mean estimate	95% CRI
SHT	2016	100	105	(90, 121)
SLT	2016	12	22	(13, 34)
STP	2016	57	69	(54, 85)
TAL	2016	NA	95	(68, 123)
WKT	2016	120	116	(99, 132)
SHT	2017	55	59	(48, 72)
SLT	2017	9	10	(6, 15)
STP	2017	48	52	(41, 64)
TAL	2017	28	31	(23, 41)
WKT	2017	105	101	(86, 117)
SHT	2018	65	42	(34, 52)
SLT	2018	8	6	(3, 9)
STP	2018	42	33	(25, 42)
TAL	2018	NA	15	(7, 27)
WKT	2018	64	58	(47, 70)

Table 4.3. Monthly cumulative precipitation (mm), average daily temperature, and average minimum daily temperature from 30-year normal trends (1981–2010 long term averages) and local monthly averages from 3 active weather stations in southwest Missouri 2016–2019.



Month	Year	P (mm)	Tavg (°C)	Tmin (°C)
Dec	30-yrN	73.2	1.8	-3.8
Dec	2016	22.9	1.6	-3.5
Dec	2017	27.5	2.5	-2.3
Dec	2018	98.4	3.6	-1.1
Jan	30-yrN	57.4	0.5	-5.3
Jan	2017	63.8	3.2	-2.0
Jan	2018	29.3	-0.5	-6.2
Jan	2019	55.6	0.7	-3.6
Feb	30-yrN	58.2	3.0	-3.1
Feb	2017	4.8	8.5	2.0
Feb	2018	120.3	3.1	-2.6
Feb	2019	57.6	1.7	-3.0

FIGURES

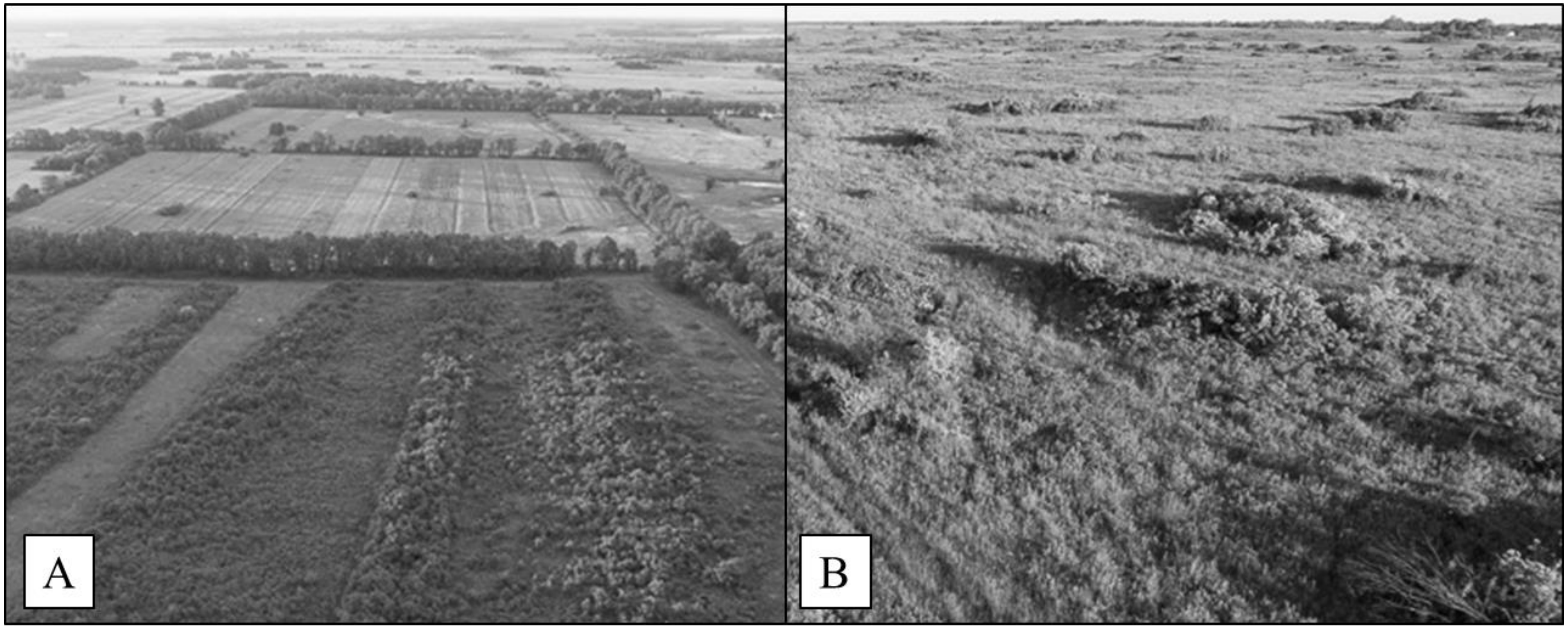


Figure 4.1. Traditional, intensively managed sites such as Talbot Conservation Area (A) employ fine-scale management practices that include agricultural strip crops and linear wooded edges among grassland units. Extensively managed sites such as Stony Point Prairie (B) are continuous remnant or reconstructed prairies that use mainly fire, grazing, and mowing to maintain early successional habitat (photos by David Stonner, MDC).

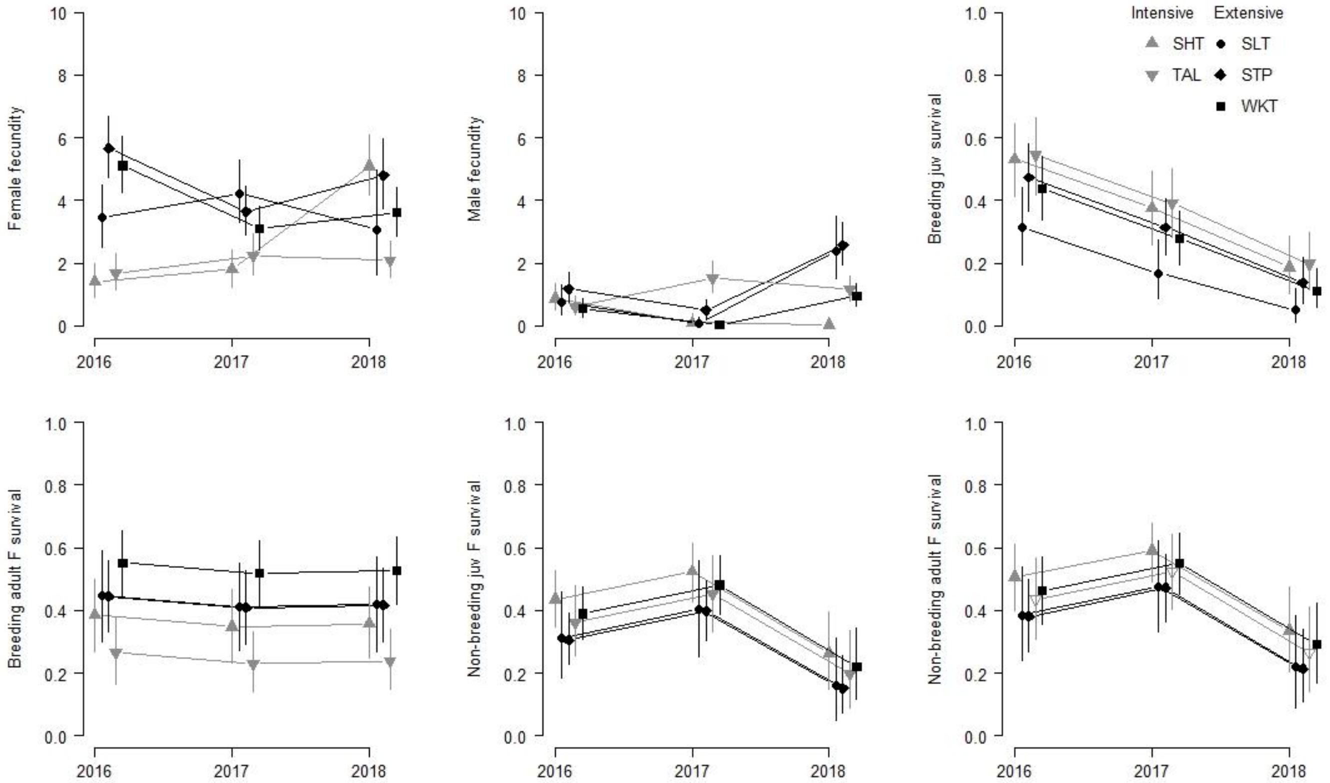


Figure 4.2. Estimated northern bobwhite population demographic rates for extensively managed sites Stony Point Prairie STP, Wah’Kon-Tah WKT, and Shelton Memorial SLT (black), and intensively managed sites Shawnee Trail SHT and Talbot TAL Conservation Areas (light grey) in southwest Missouri. Top left: female fecundity, or the average number of eggs hatched per female-incubated nest for all sites and years; center: male fecundity; right: juvenile breeding season survival estimates (1 May–31 Oct) for each site 2016–2018. Bottom left: adult female breeding season survival estimates (1 May–31 Oct); center: juvenile female non-breeding season survival (1 Nov–31 Apr); right: adult female non-breeding season survival estimates (1 Nov–31 Apr) for each site 2016–2018.

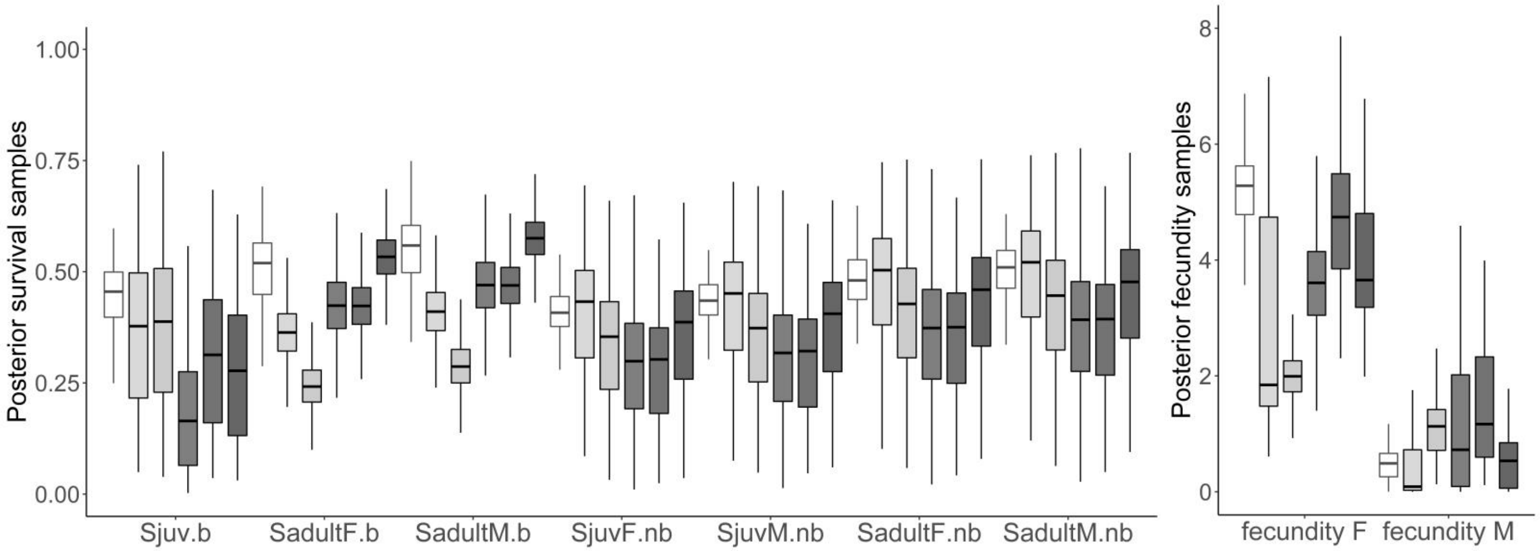


Figure 4.3. Posterior distributions of Northern bobwhite seasonal survival and fecundity estimates across all years for each site in southwest Missouri. The first box plot for each vital rate represents a subset of posterior samples that resulted in a stable population growth rate (white; λ > 1.00). Observed site-level vital rates are then given in the following order for each vital rate: Shawnee Trail and Talbot (light grey, intensively managed sites), then Shelton Memorial, Stony Point Prairie, and Wah’Kon-Tah Prairie (dark grey, extensively managed sites). Posterior distributions of survival (S) are shown for juveniles (juv), adults, females (F), and males (M) for the breeding (b) and non-breeding (nb) seasons. Posterior fecundity distributions for number of young hatched per female-incubated nests (fecundity *F*) and male-incubated nests (fecundity M).

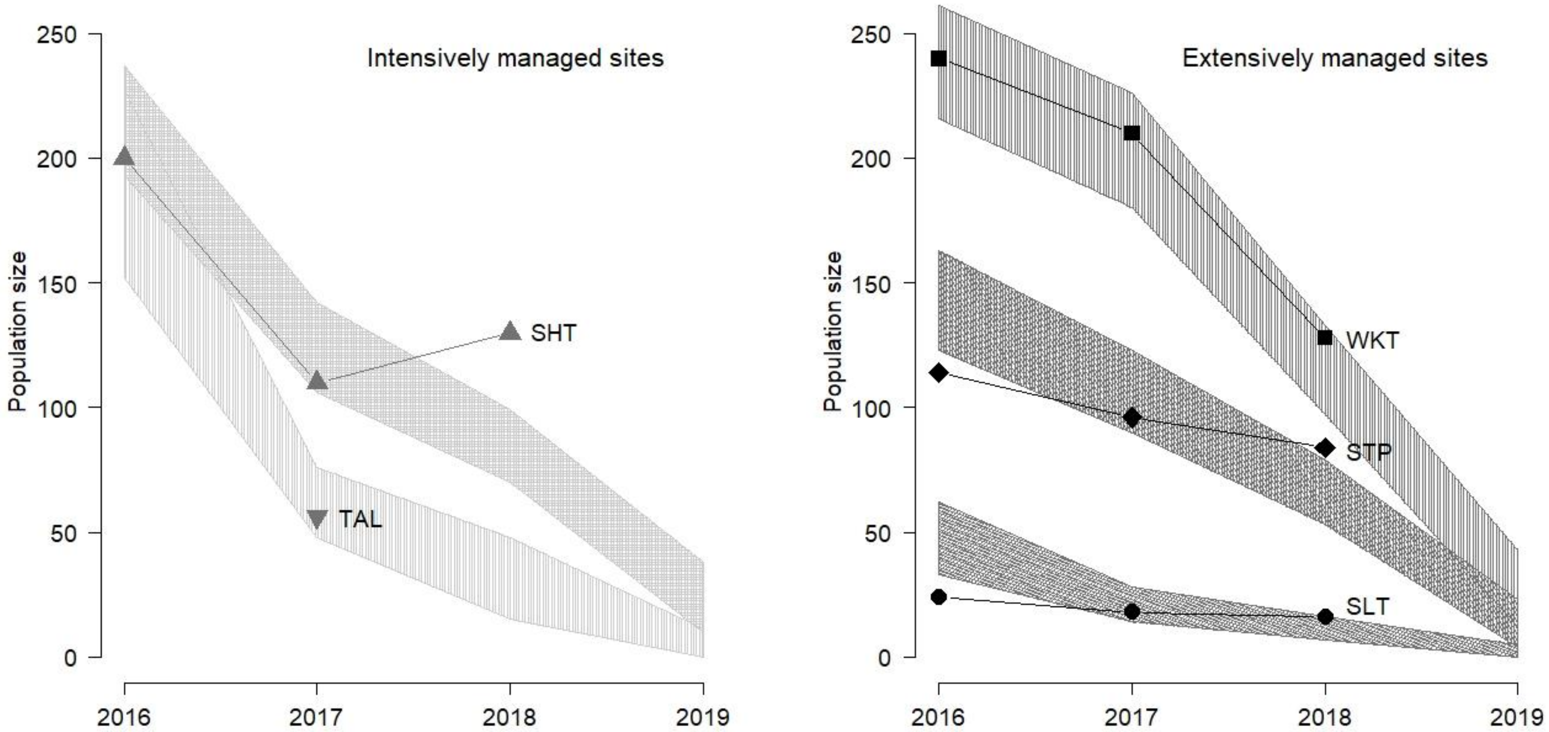


Figure 4.4. Northern bobwhite population counts (points) and estimated abundances (ribbons) for the two intensively managed sites Shawnee Trail SHT and Talbot TAL Conservation areas (left; light grey), and the three extensively managed sites Stony Point Prairie STP, Wah’Kon-Tah WKT, and Shelton Memorial SLT (right; dark grey), and in southwest Missouri 1 May 2016–2018.

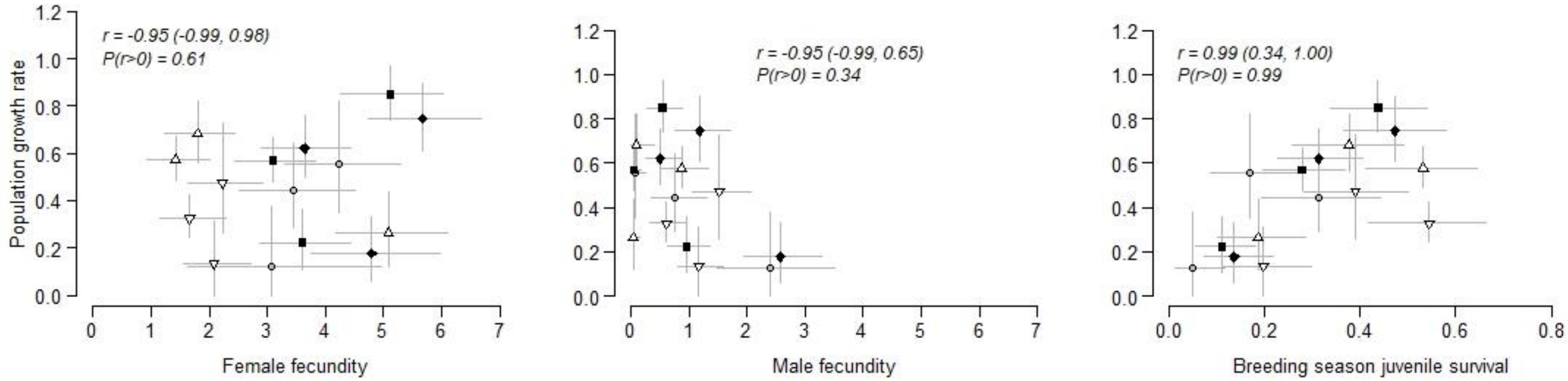


Figure 4.5. Fecundity and breeding season juvenile survival probability estimates for northern bobwhite plotted against estimates of interannual population growth rates for the two extensive native grassland sites Stony Point and Wah'Kon-Tah (black), the small prairie Shelton Memorial (grey), and the two intensively managed conservation areas Shawnee Trail and Talbot (white) in southwest Missouri. Points display mean estimates and grey lines show 95% CRI. Also correlation coefficients (*r*, with 95% CRI) and the probability of a positive correlation (P(*r*>0)) are estimated across posteriors for all sites and all years.

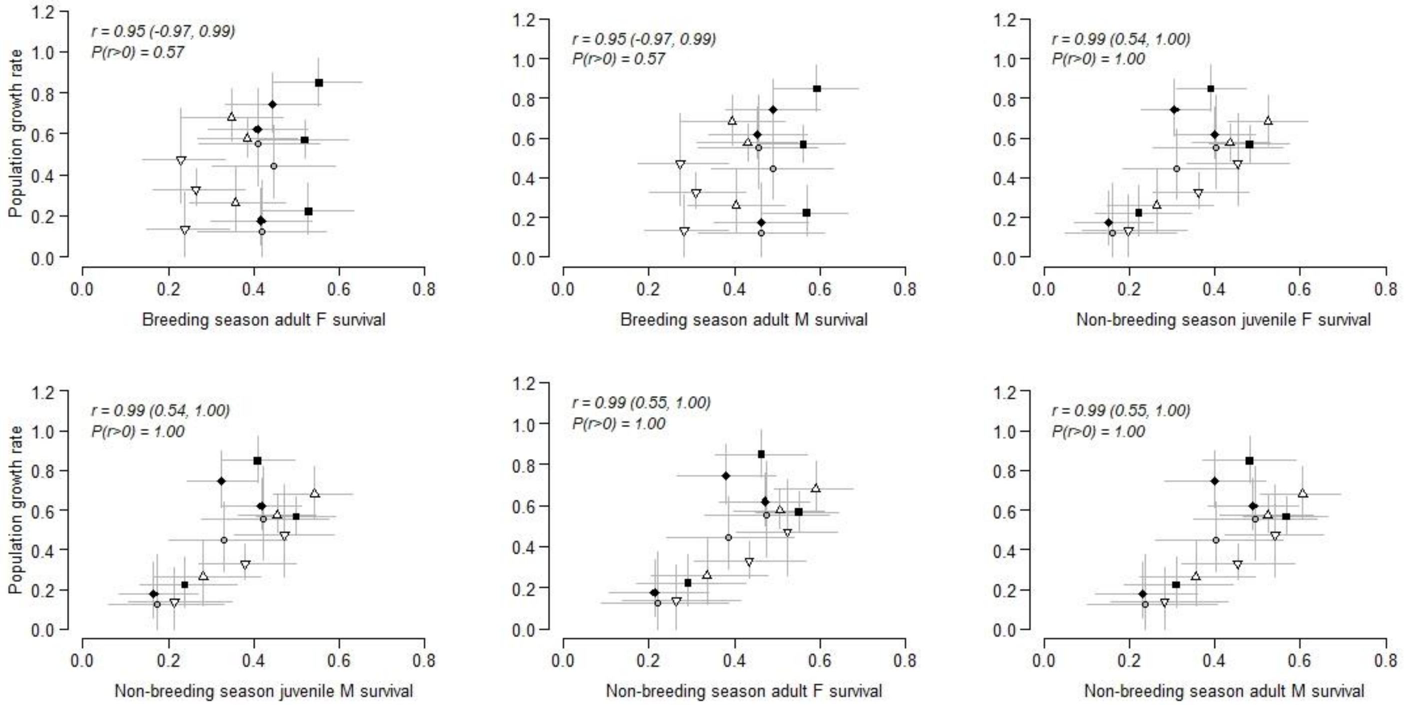


Figure 4.6. Seasonal survival probability estimates for northern bobwhite plotted against estimates of interannual population growth rates for the two extensive native grassland sites Stony Point and Wah'Kon-Tah (black), the small prairie Shelton Memorial (grey), and the two intensively managed conservation areas Shawnee Trail and Talbot (white) in southwest Missouri. Points display mean estimates and grey lines show 95% CRI. Also correlation coefficients (*r*, with 95% CRI) and the probability of a positive correlation (P(*r*>0)) are estimated across posteriors for all sites and all years.

VITA

Emily Ann Sinnott is interested in applied wildlife ecology research. Emily was born in St. Louis, Missouri and raised in Tokyo, Japan. She received her B.A. from Colby College where she double majored in Biology and Environmental Studies with a concentration in Policy. After her undergraduate studies, she spent several years in the field as a wildlife technician, mainly in the desert southwest. She earned her M.S. in Natural Resource Ecology and Management from Oklahoma State University in Dr. Timothy O’Connell’s lab where she studied forest songbird communities at the western edge of their breeding range. In 2016 she began working at University of Missouri on Missouri’s southwest quail study examining brood ecology and full annual cycle population dynamics with Dr. Frank Thompson III and Dr. Mitch D. Weegman.